A DESCRIPTION OF THE VERTEBRAL COLUMN OF *ERYOPS* BASED ON THE NOTES AND DRAWINGS OF A. S. ROMER

JAMES M. MOULTON[1]

ABSTRACT. This paper includes an illustrated description of the vertebral column and ribs of *Eryops megacephalus* Cope, based principally on notes and drawings prepared by A. S. Romer. The paper examines closely regional variation in the column. The descriptions, originally written of the *Eryops* now mounted in the Museum of Comparative Zoology (MCZ 1539), are amplified by reference to other specimens. The paper includes data on growth stages and regional variation in the vertebral column and ribs, which will be useful in interpretation of *Eryops* postcranial remains.

INTRODUCTION

This publication was to have been based on collaborative work with Alfred S. Romer, but his untimely death on November 5, 1973 prevented this. Fortunately, his notes and drawings on the postcranial anatomy of *Eryops* have been available to me and are here incorporated; his handwritten descriptive working notes are only slightly modified. The paper presents a generalized description of the vertebral column of *Eryops*, and drawings of a set of presacral and postsacral ribs. The principal concern in preparing this material has been that Professor Romer's observations should be available to paleontologists. To Professor Romer's observations, I have added others which appear to be of interest.

Gregory (1951, I: 253) called *Eryops* "the best known" of all rhachitomous labrinthodonts; Williston (1914) called it "the most famous" of the Temnospondyli. But despite the detailed descriptions of various parts — skull (Sawin, 1941), teeth (Stick-

[1]Department of Biology, Bowdoin College, Brunswick, Maine 04011.

ler, 1899), forelimb (Miner, 1925), ilio-sacral attachment (Olson, 1936a) — no account of the vertebral column as a whole is available.

In familiarizing myself with *Eryops* material, I gratefully acknowledge the help of discussions with Ernest E. Williams, Nelda Wright, Robert L. Carroll, Thomas S. Parsons, John R. Bolt, Keith S. Thomson, Bryan Patterson and Bobb Schaeffer, and to Carroll, Patterson, Williams and Wright I extend thanks for critical reading of all or of large portions of my manuscript. I appreciate the opportunity to study specimens in the following institutions: the Redpath Museum of McGill University with Dr. Carroll, the Cleveland Museum of Natural History (CMNH) through David H. Dunkle, the Field Museum of Natural History (FMNH) through Dr. Bolt, the Peabody Museum of Yale University through Dr. Thomson, the American Museum of Natural History (AMNH)) through Eugene S. Gaffney, and the Pratt Museum of Amherst College through Walter P. Coombs; and I was aided by valued correspondence with several of those mentioned above and also with Robert E. DeMar, Everett C. Olson, A. L. Panchen, F. R. Parrington and Peter P. Vaughn. A loan of *Eryops avinoffi* material from the Cleveland Museum is gratefully acknowledged.

The staff of the Museum of Comparative Zoology, and especially Professors A. W. Crompton and Farish Jenkins, Jr., Director and Associate Curator of Vertebrate Paleontology, have been very generous with their hospitality and have made the Museum a most rewarding place to work during spring term of 1973–74. I am indebted for travel and research funds to Bowdoin College.

Eryops material has been described from the Carboniferous and Permian of an area extending from New Mexico to Prince Edward Island (Langston, 1953, 1963; Olson and Vaughn, 1970), the bulk of it from the lower Permian of Texas where it is the common large form (Romer, 1958). Both the geological range occupied by *Eryops* and the length of time it survived are grounds for suspecting that more than one *Eryops* species existed (Williston, 1914; Romer, 1943, 1947, 1952). But in the absence of a sound anatomical basis for separating species (Romer, 1947, 1952; E. C. Olson, personal communication), the bulk of *Eryops* material from the Permian is now generally assigned to *Eryops megacephalus* Cope, 1877. Appreciation of the extent of speciation in *Eryops* must await a distinction between specific differences and those due to growth and accidents of preserva-

tion. Recognized as a distinct species, however, is *Eryops avinoffi* (Romer) from the Pennsylvanian of West Virginia and lower Permian of Pennsylvanian (Romer, 1952; Vaughn, 1958). Photographs of its dorsal vertebrae have been published (Murphy, 1971).

It is to Cope then that we are indebted for the original description of *Eryops* from Texas Permian material collected by Jacob Boll, his friend and collector (Cope, 1877; Osborn, 1931: 486), and himself a recognized scientist (see e.g. Broili, 1899: 61) and practicing geologist. Born in Canton Aargau, Switzerland on May 29, 1828, Boll died alone of appendicitis in a tent on the Pease River near its confluence with the Red River in Texas on September 29, 1880 (A. S. Romer, personal communication), lamented by his friend Cope (1884). *Eryops* material was given a prominent place in Cope's collection (Osborn, 1931: frontispiece; 587) and figured frequently in his publications. Cope's paleontological collections, purchased for the American Museum of Natural History (*idem*, Chapter 6), included materials Boll had collected. One specimen, AMNH 4183, from which I believe Cope's most frequently reproduced figures of vertebrae were drawn (see, for example, Cope and Matthew, 1915), is still accompanied by Boll's penciled, signed field label dated 1–12–80 from the North Fork of the Little Wichita River, which, together with the Big Wichita, Boll explored scientifically for over six months from December, 1879 (Boll, 1880). While studying this material in the American Museum collections on March 28, 1974, I happened to turn over the old field label, and there was a penciled poem, also signed 'Boll', which read as follows:

> "Nun wirst du mit noch manchen andern
> Zum Sitze des Professors wandern.
> Geistreich denkend wird er dich erwecken,
> Aus deinen Trümmern dich zusammensetzen.
> Der Nachwelt wird er dann erzaehlen,
> Wie du gebaut in deinen Zähnen,
> Wie du gelebt und wie verschwunden,
> Benennen dich und was gefunden."

For help in transcription, I am indebted to B. Werscheck of the American Museum of Natural History.

Cope's publications dealing significantly with the vertebral column of *Eryops* appeared in the years 1877, 1880 (a,b), 1881, 1882, 1884, and 1890, a number of them repeating the same

left lateral and ventral views of portions of the vertebral column which first appeared in 1880 (Cope, 1880b); some of Cope's discussions of rhachitomous vertebrae (1878a,b; 1897; 1898) omitted them, but they finally appeared in Cope and Matthew (1915). Later diagrams of *Eryops* vertebrae or of generalized rhachitomous vertebrae, often drawn to emphasize particular points, are seldom more convincing than those Cope drew 'from life'.

Cope (1880a,b; 1881), Broili (1899), Branson (1905), Case (1911, 1915), Williston (1918), Watson (1919), Olson (1936b), Rockwell, Evans and Pheasant (1938), Romer (1947, 1966), Gregory (1951), Panchen (1967, Parrington (1967), Thomson and Bossy (1970), and Williams (1959) collectively provide a description of the *Eryops* vertebral column and its evolution, often with special attention to typical dorsal vertebrae. The papers of Cope (1880b) and Case (1911) provide the most complete accounts. Further, a paper on another rhachitome, *Edops* (Romer and Witter, 1942), makes several points about the vertebrae of *Eryops* and provides a measure of differentiation within the rhachitomes. A photograph of *Eryops* caudal vertebrae from the MCZ mount (MCZ 1539) has been published (Romer and Witter, 1941) with a description of dermal scales (see also Williston, 1915); caudal vertebrae have also been illustrated by Cope (1890). Diagrams of *Eryops* and other rhachitomous vertebrae are generally shown in lateral view; it is not easy to comprehend the three-dimensional form without the actual specimen in hand. The deficiency of anterior and posterior views is corrected by several of Romer's figures in the present paper. Anterior views of dorsal vertebrae are provided by Broili (1899) and Rockwell *et al* (1938). Branson (1905) and Cope (Cope and Matthew, 1915) show the atlas in anterior view, while Cope (*idem*) and Olson (1936b) show side views of atlas and axis, articulated and disarticulated respectively; Cope (*idem*) shows a somewhat distorted atlas (AMNH 4183) articulated with the axis in anterior view. Photographs of mounted *Eryops* skeletons have been published (Miner, 1926; Romer, 1943), as well as drawings of the entire skeleton (Case, 1911; Gregory, 1951).

An illustrated description of the whole vertebral column and ribs had long been planned by Romer (1943, 1947, 1958). His drawings with others showing particular points are here presented with a description prepared largely from his handwritten
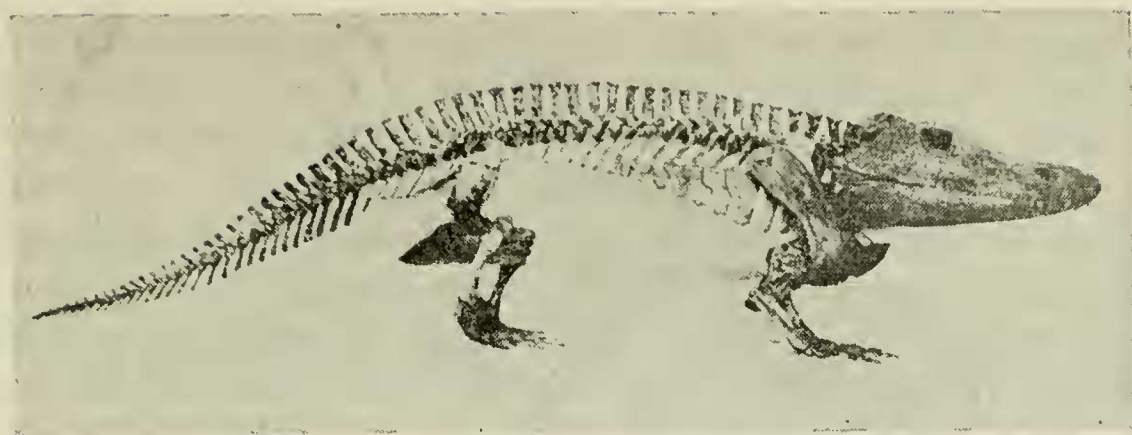
Plate I. Mounted skeleton of *Eryops,* MCZ 1539 (from Romer, 1943). × 1/21.

notes. Observations on variations in size and form in *Eryops* vertebrae are also included. A future study should focus on vertebral growth in *Eryops megacephalus,* a matter of considerable interest only touched on in the present paper. This paper examines variation in structure throughout the vertebral column, and reconstructs the probable structure in life of the vertebral column of *Eryops* from the dissociated jumble of neural arches, pleuro- and intercentra to which the vertebral column of *Eryops* and other rhachitomes is often reduced in the fossil state.

The *Eryops* mount in the Museum of Comparative Zoology (Plate I), the "most perfect (skeleton) yet discovered" (Romer, 1943), is a not quite full-grown animal (A. S. Romer, personal communication). Vertebrae of larger size and more massive construction than those in the mount are not uncommon in the collections I have studied. The MCZ mount is however comparable in size to similar mounts in the Cleveland, Field, Peabody, American and Pratt Museums collected over a considerable span of years, suggesting that full-grown (or larger species) of *Eryops* for some reason lent themselves less well to preservation or were rarer than smaller animals. The specimen in the Pratt Museum, from Geraldine, Texas, is probably the youngest of the mounts studied; it is somewhat smaller than the MCZ mount which measures over the tops of the neural spines 187.5 cm muzzle to tail tip, with a presacral vertebral column of 71.9 cm and a postsacral length of 80.6 cm. The skull measures 35 cm.

From well-preserved *Eryops* material such as that which furnished the mounts for the MCZ and Pratt Museum, Romer (personal communication) was able to "make outlines of the whole set of vertebrae, clear to the tip of the tail, and each rib";

drawings from those outlines illustrate this article. Complete tails and even complete presacral series of *Eryops* vertebrae have not been common finds, and understandably controversy has arisen over tail lengths and vertebral numbers. The MCZ mount is taken to be correct until better information is available; it displays 22 presacral vertebrae, two less than the primitive number (Romer, 1947; Vaughn, 1971), and 37 postsacral vertebrae, a total, with the single sacral, of 60. The paired proatlas atop the bisected atlas is well shown in its correct relationships in the Field and Pratt mounts (Fig. 1). Presacral-postsacral counts of five other *Eryops* mounts are: 22 — 44, 21 — 51, 22 — 30, 22 — incomplete postsacral series, and 22 — 46.

With Case (1915) we are inclined to believe that the bifurcated caudal spines in *Eryops* provided dorsal accommodation for tendons, which in primitive forms are the chief support of the axial column (Olson, 1936b); the *Eryops* arrangement suggests a tail of reasonable length which may have been held off the ground. Tail length in *Eryops* should be resolved because it is of significance in understanding locomotion. Former estimates have varied from Cope's of a medium-length tail (1880b) to a stump nearly coccygeal (1884), the latter seconded with some reservation by Case (1915), to Williston's admission of ignorance and his drawing of *Eryops* with its tail concealed by vegetation (Williston, 1914). Romer's orthometric linear unit (Panchen, 1966) has not been applied to *Eryops* in estimating a length for the tail.

The following descriptions unless otherwise stated are based on vertebrae in the MCZ and Pratt Museum mounts of *Eryops*.

PRESACRAL VERTEBRAE BEHIND THE AXIS (DORSAL VERTEBRAE)
(Figs. 1–4; 9 I; 10; 11; measurements in Table 1)

Each vertebra consists of four ossifications: neural arch, paired pleurocentra behind the neural arch and a single intercentrum ahead and below. The neural arch terminates dorsally in a neural spine that, for an amphibian, is of considerable height. In a mid-dorsal, the height of the spine above a line through the center of the zygapophyses is 56 mm, when the vertebral length is 35 mm, a ratio of 1.6. Spine height increases to 73 mm in the last presacral, and the height-length ratio approaches 2. There is a gradual decrease in spine height anteriorly — it being
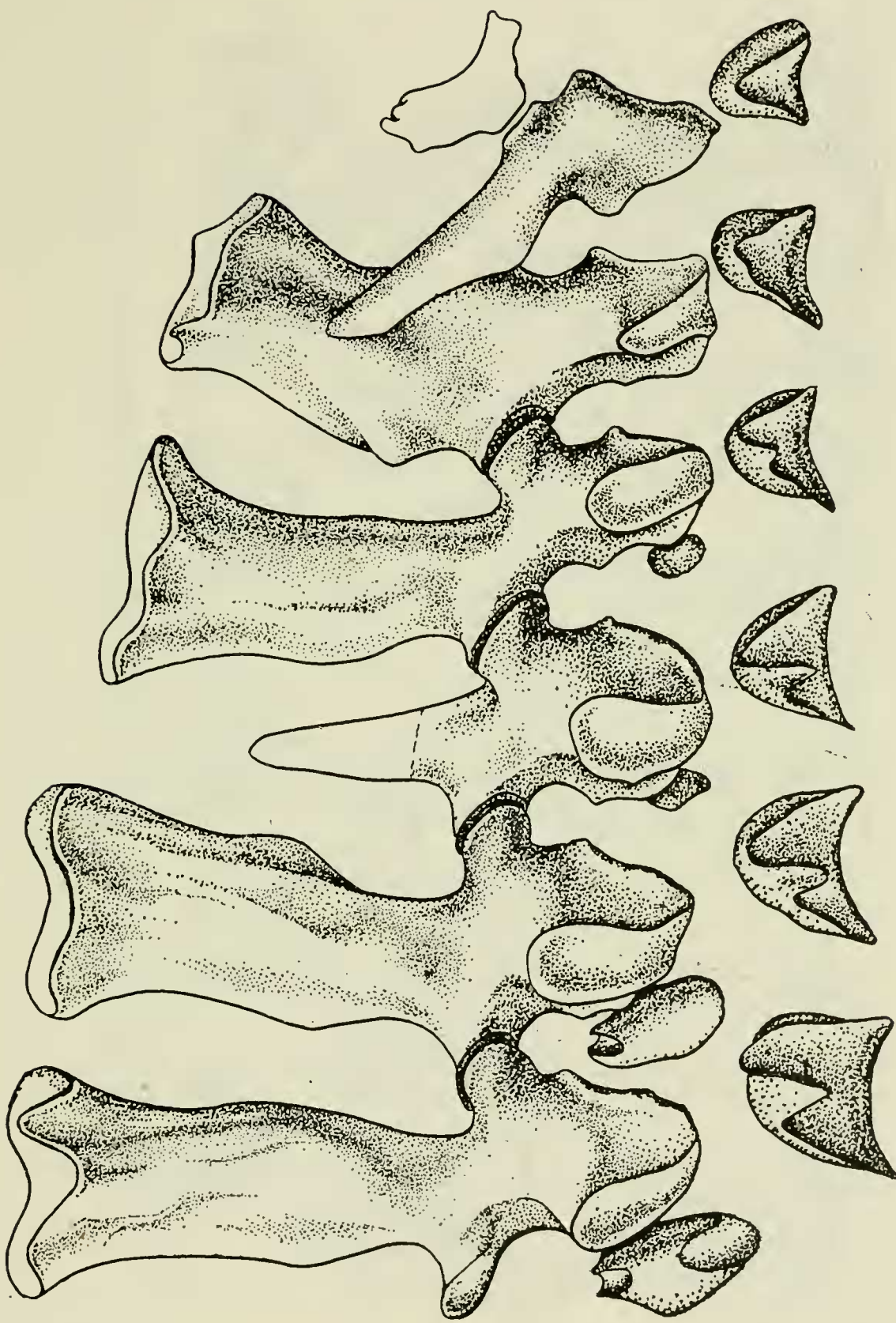
Figure 1. The presacral vertebral column of *Eryops*, anterior to the right: Proatlas, atlas, axis and vertebrae 3–6, × .9.
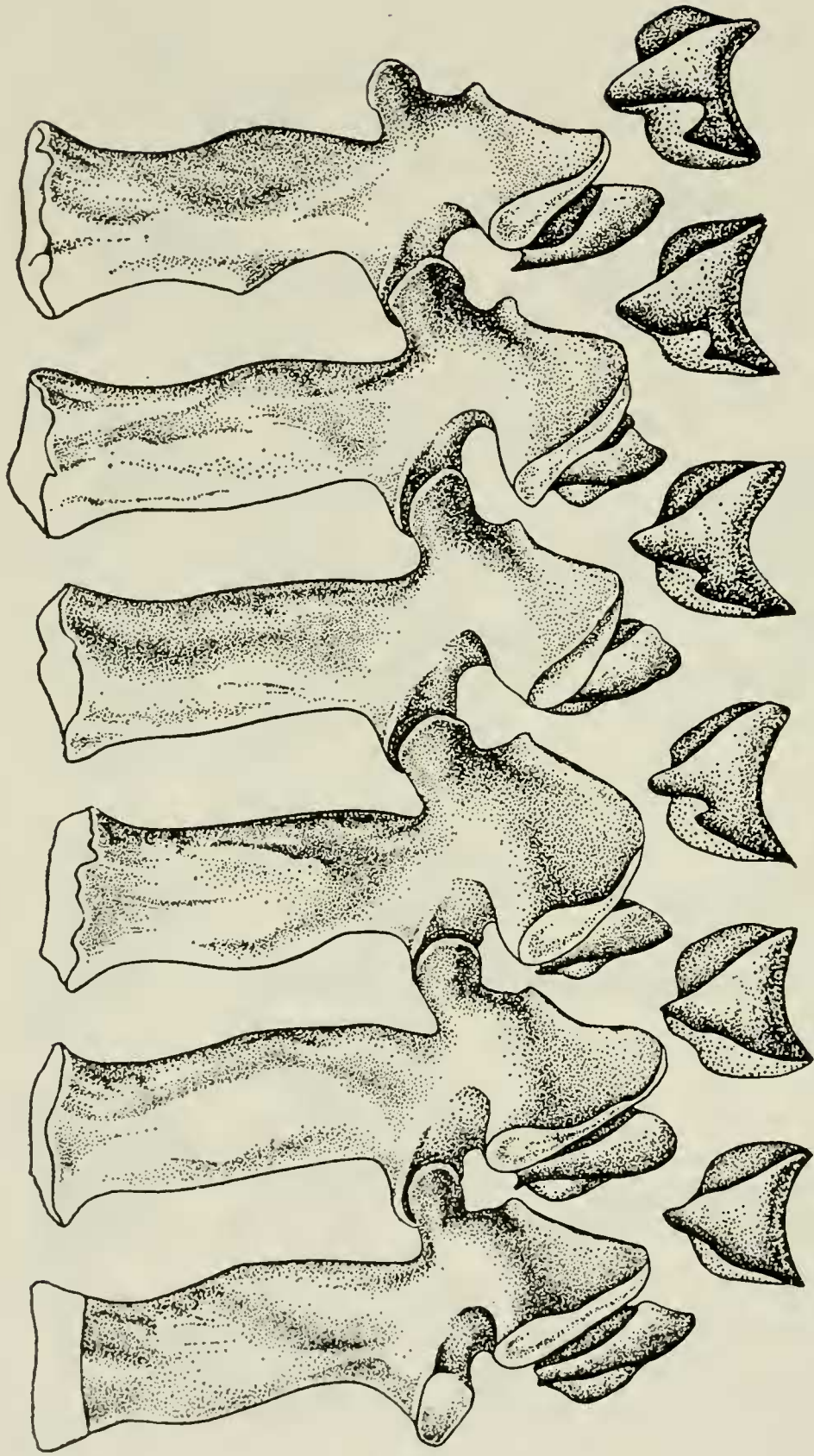
Figure 2. The presacral vertebral column of *Eryops*, vertebrae 7-12, × .7.
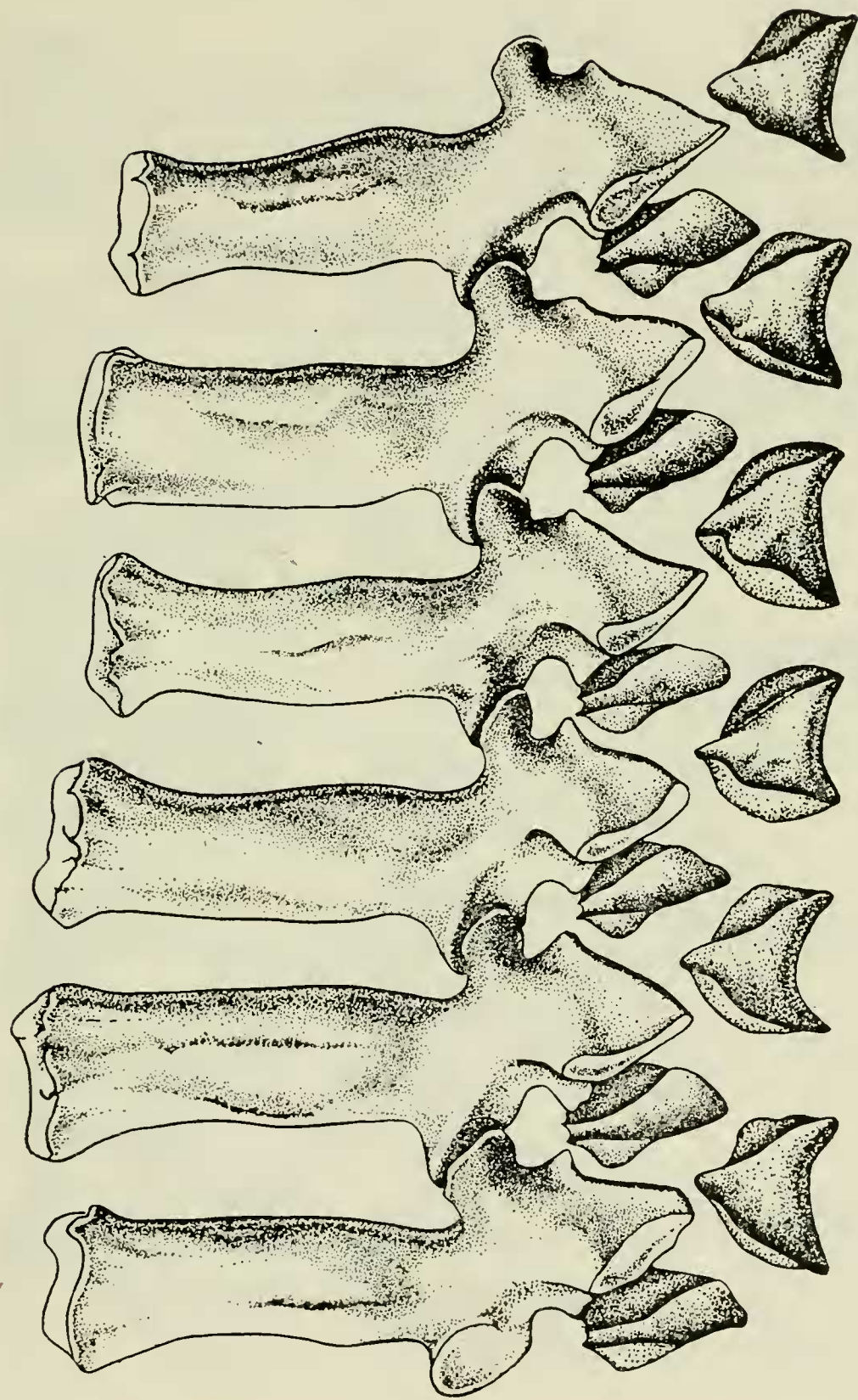
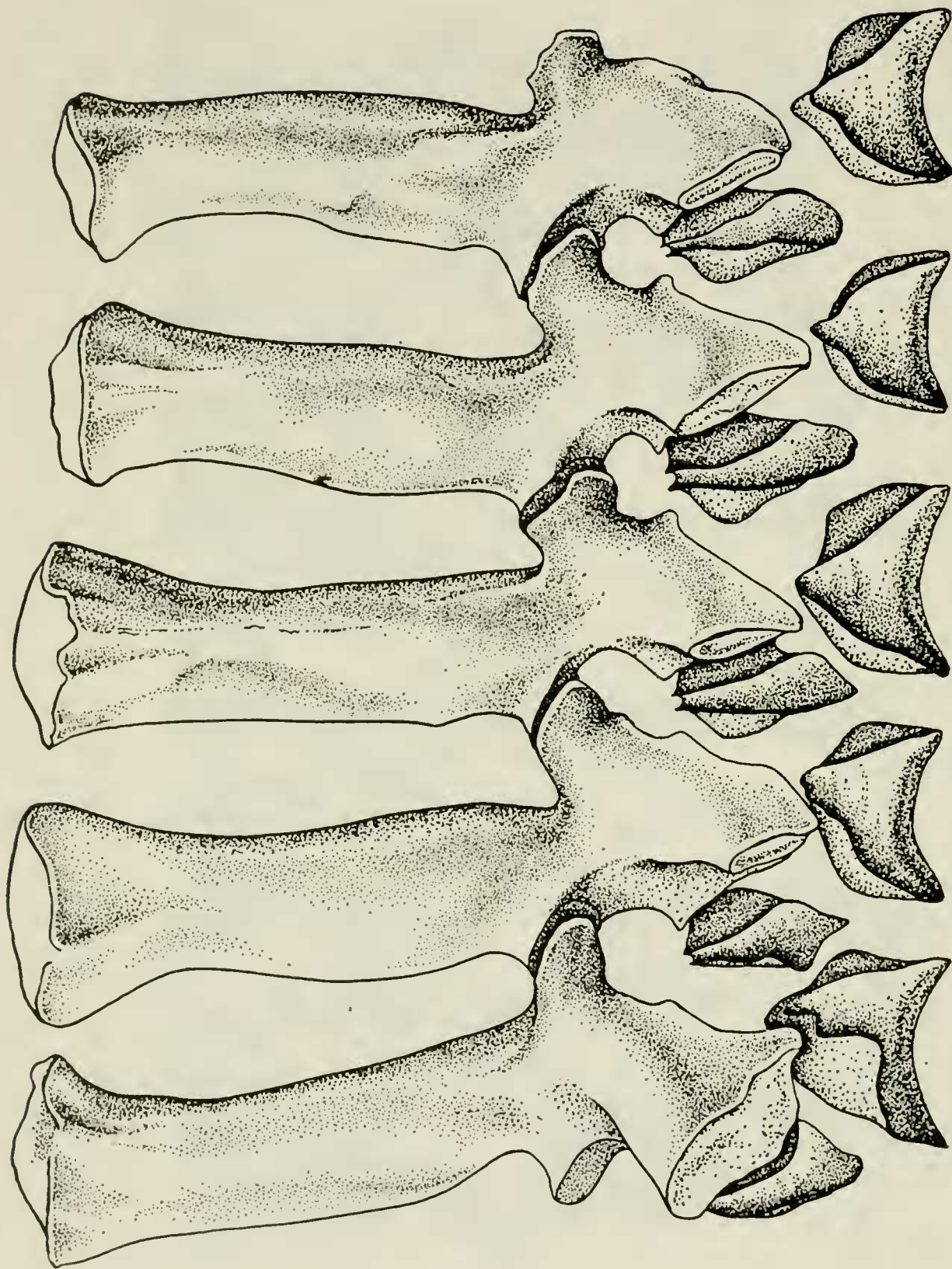Figure 3. The presacral vertebral column of *Eryops*, vertebrae 13–18, × 7.

Figure 4. The presacral vertebral column of *Eryops*, vertebrae 19–23 (sacral vertebra), × .7.
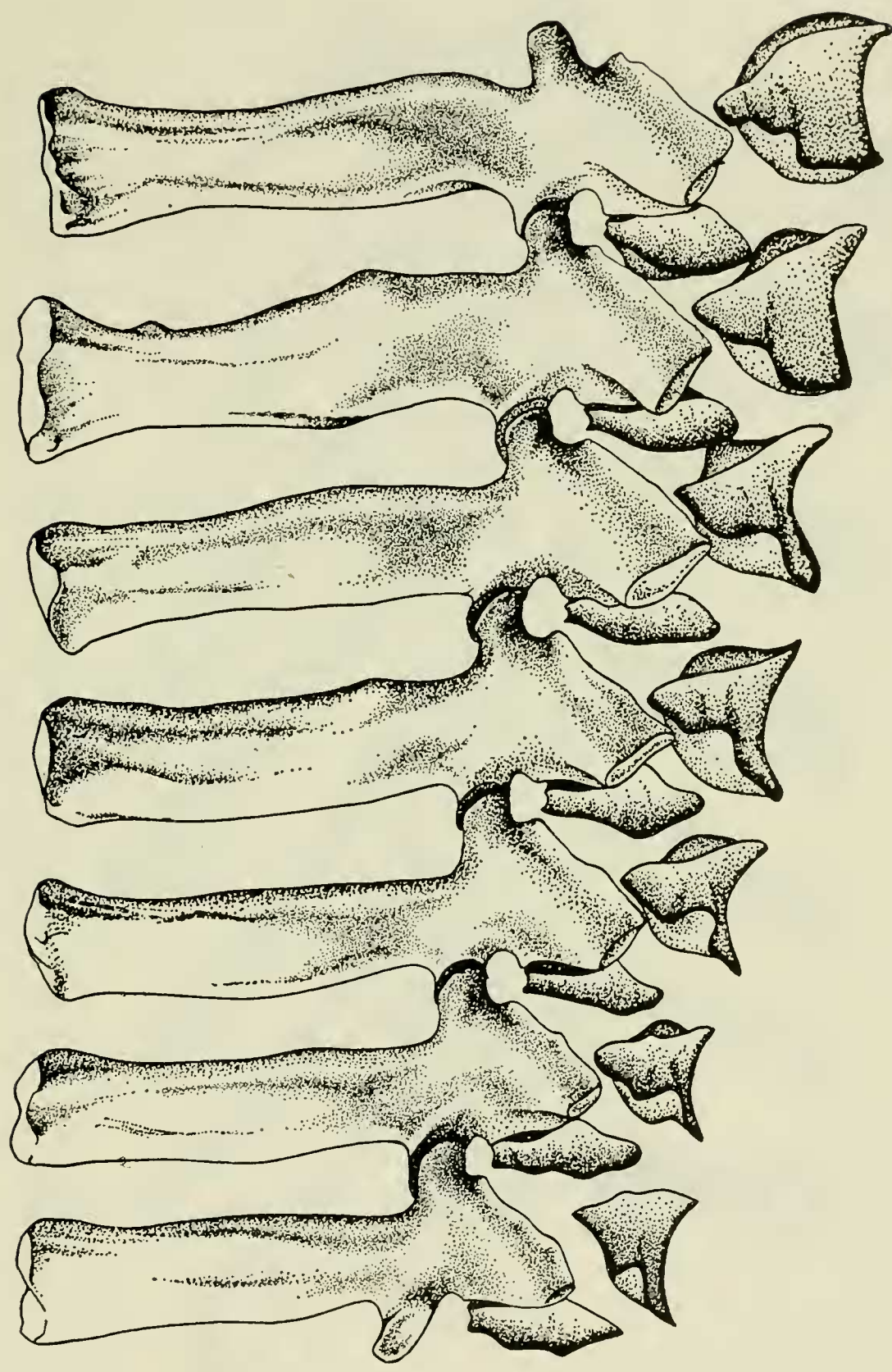
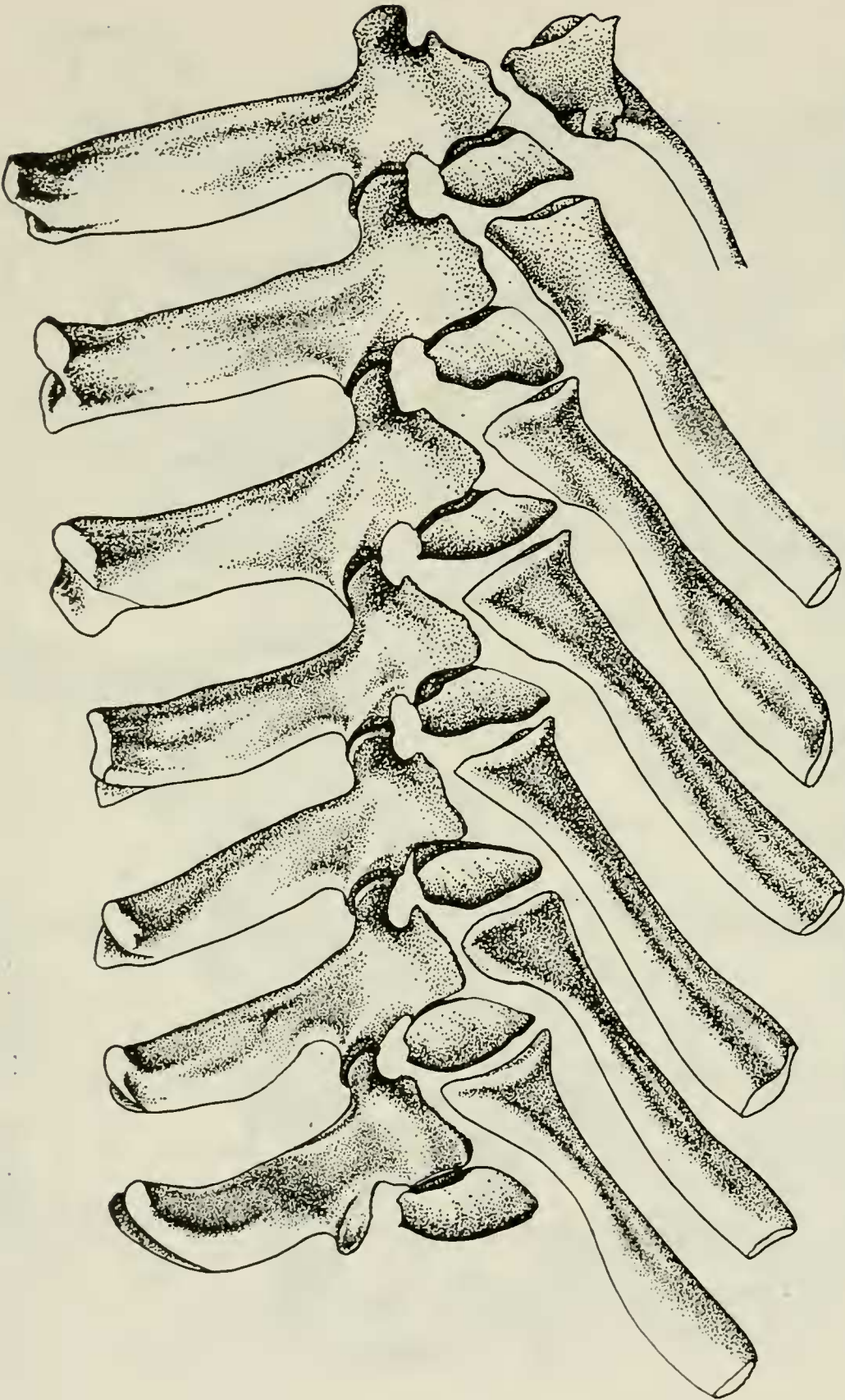Figure 5. The postsacral vertebral column of *Eryops*, vertebrae 24–30, × .7.

Figure 6. The postsacral vertebral column of *Eryops*, vertebrae 31–37, × .7.
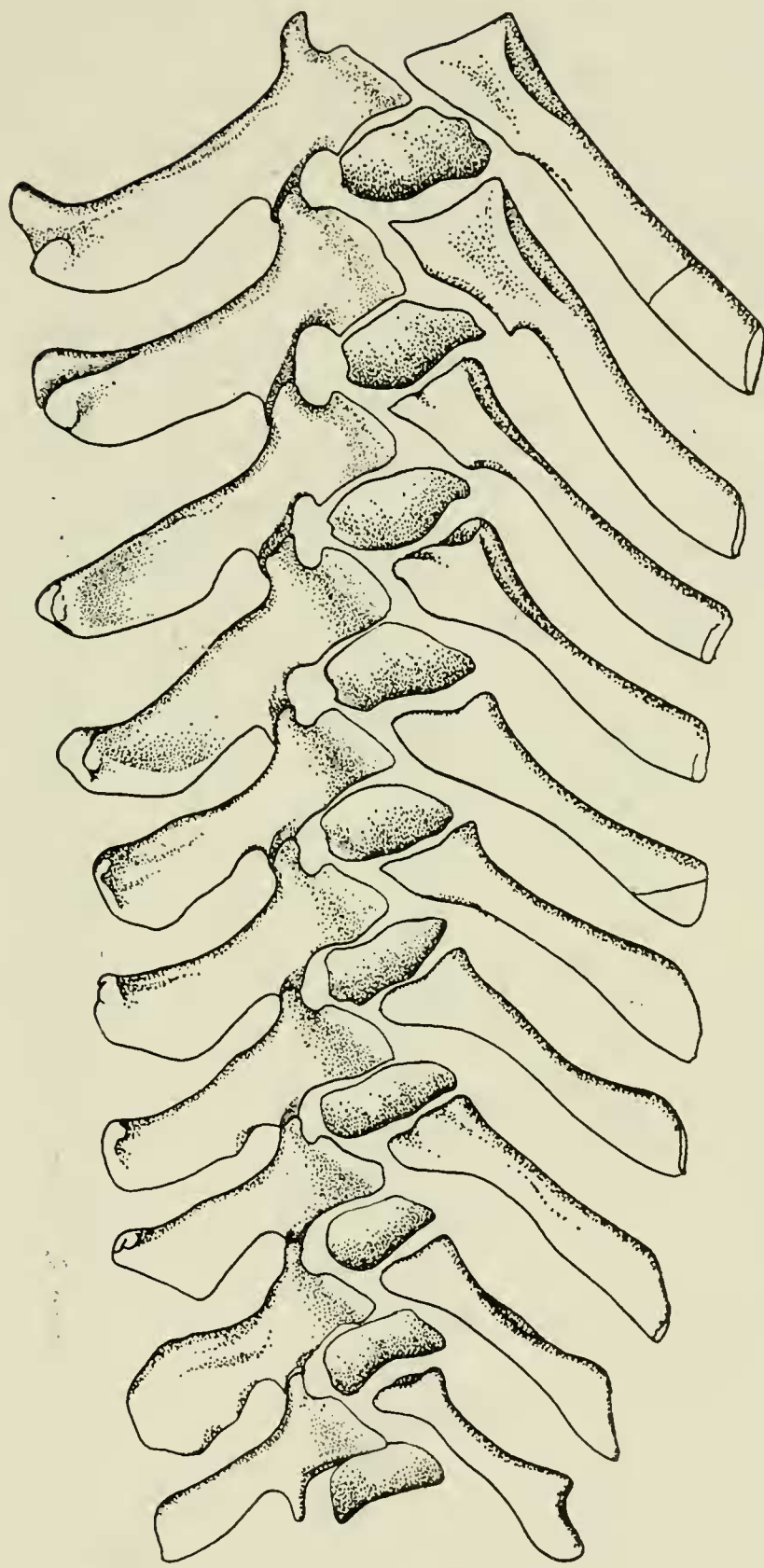
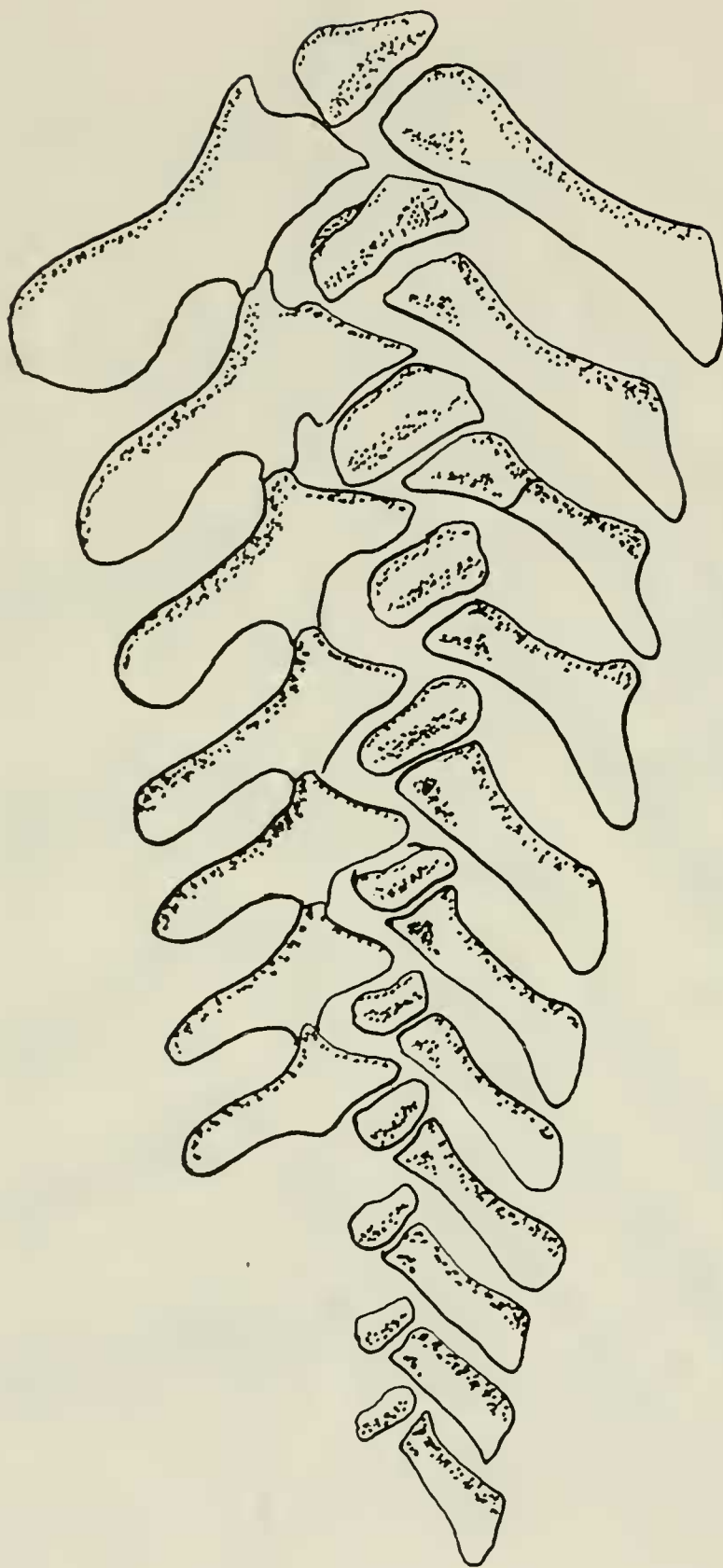Figure 7. The postsacral vertebral column of *Eryops*, vertebrae 38-47, × .7.

Figure 8. The postsacral vertebral column of *Eryops*, vertebrae 48–58, × 1.

57 mm in vertebra 5 — and a rather sharp decrease associated with transition to the skull, it being 44 mm at the axis.

In reasonably mature specimens, the tops of the spines become expanded, subcircular and rugose; they surely lay in the dermis. The appearance in some cases is of dermal ossifications fused to the spine tips (Fig. 14 B), but there is no evidence of separate ossifications. Expanded spine tips may be lacking in young specimens. The width of the spine shaft is about 2/3 of the anteroposterior dimension, although sometimes the neural spines are considerably more flattened than this. The spines often assume a diamond form in cross-section with lateral ridges in the upper part which expand into the sides of the dorsal rugosity.

Minor spines, spurs and flanges are not uncommon on neural spines and elsewhere (Fig. 9 I; two spines on a neural spine, AMNH 4183; spine on transverse process of vertebra 18, AMNH 4280; flange on spine of postsacral 10, MCZ 1539). Some of these may be artifacts of preservation, as is undoubtedly the flattening observed in some neural spines. A remarkable flexibility of *Eryops* skeletal material either shortly after death because of drying cartilage (see p. 22) or changes during preservation is suggested by the twisted neural arches and spines one not infrequently encounters in collections (Fig. 9 D; sacral vertebra of MCZ 2669, for example).

The upper part of the neural spine is keeled both anteriorly and posteriorly. In the lower part of the spine, the keel bifurcates into two divergent ridges which pass into the zygapophyses ventrally. Secondary ridges may be present within the groove enclosed by the ridge pairs. Both grooves tend to become reduced in depth in very large vertebrae. The anterior groove may extend more than halfway up the spine, more so in the anterior part of the vertebral column than posteriorly. In the last presacrals, the anterior groove is limited to 1/3 of the spine height and becomes relatively shallow. The point of bifurcation of the ridges at the top of the grooves is often recognizable in side view by a marked angularity in the contour of the spine, and the spine shaft is broadest between these points. The posterior groove deepens ventrally into a deep pit between the posterior zygaphophyses.

The zygaphophyses are of the normal primitive tetrapod type and are readily comparable with, for example, those of many pelycosaurs in size, contours, inclination and relative position. As usual in labyrinthodonts and pelycosaurs, but in contrast to
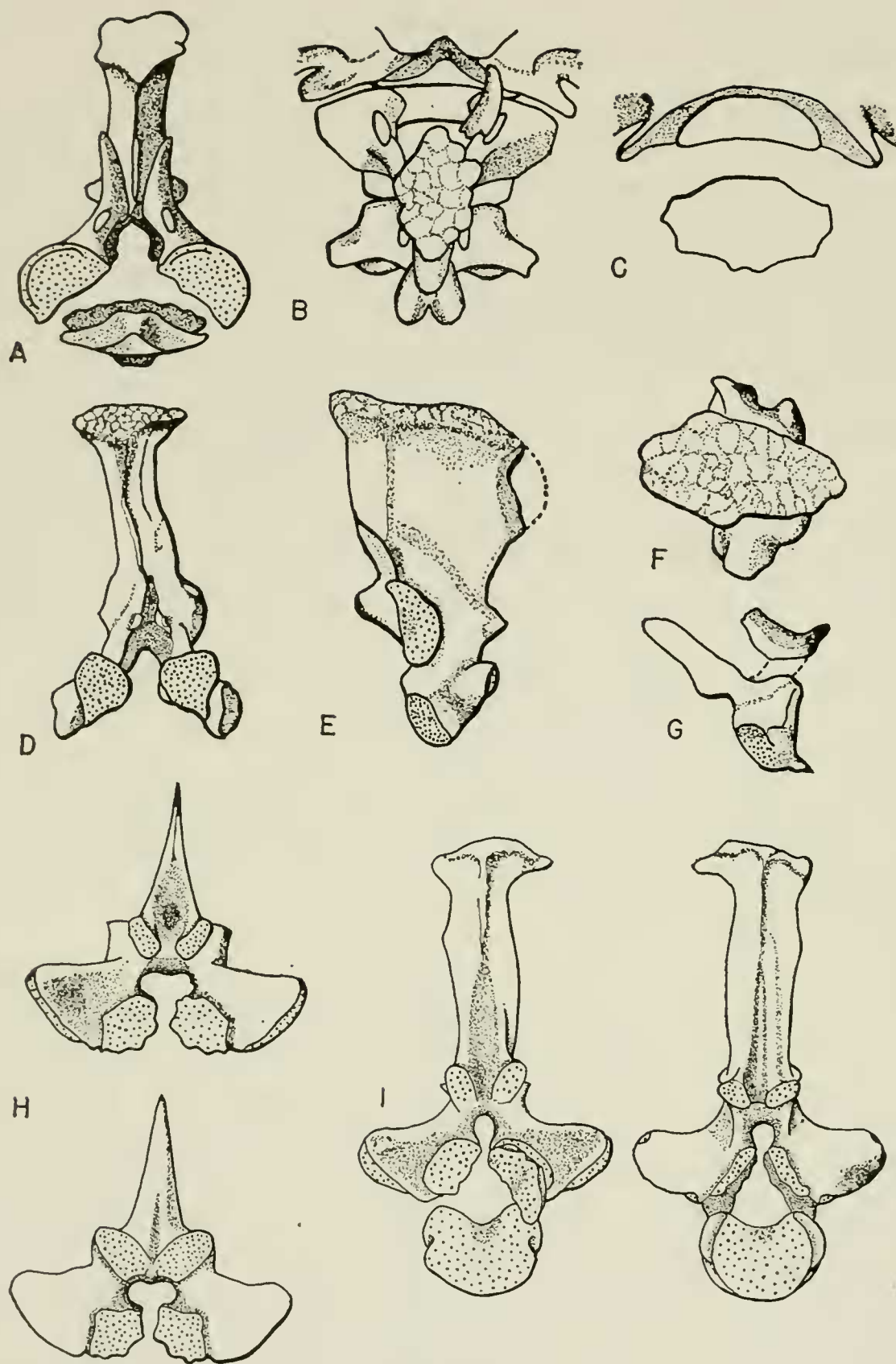
Figure 9. Based mainly on *Eryops* MCZ 1539 and 1883, all × .5. (A) Atlas and axis with their intercentra, in anterior view, proatlas removed. (B) *Eryops* occipital region, atlas, axis and right proatlas, anterior at top. (C) *Eryops* occipital region from below showing anterior intercentra. (D) *Eryops* axis MCZ 1883, anterior view. (E) *Eryops* axis MCZ 1883, right lateral view, anterior flange reconstructed. (F) *Eryops* axis MCZ 1883 in dorsal view. (G) *Eryops* atlas and proatlas, left elements from medial side. (H) *Eryops* vertebra 4, posterior (above) and anterior views. (I) *Eryops* vertebra 6, posterior (l.) and anterior views.
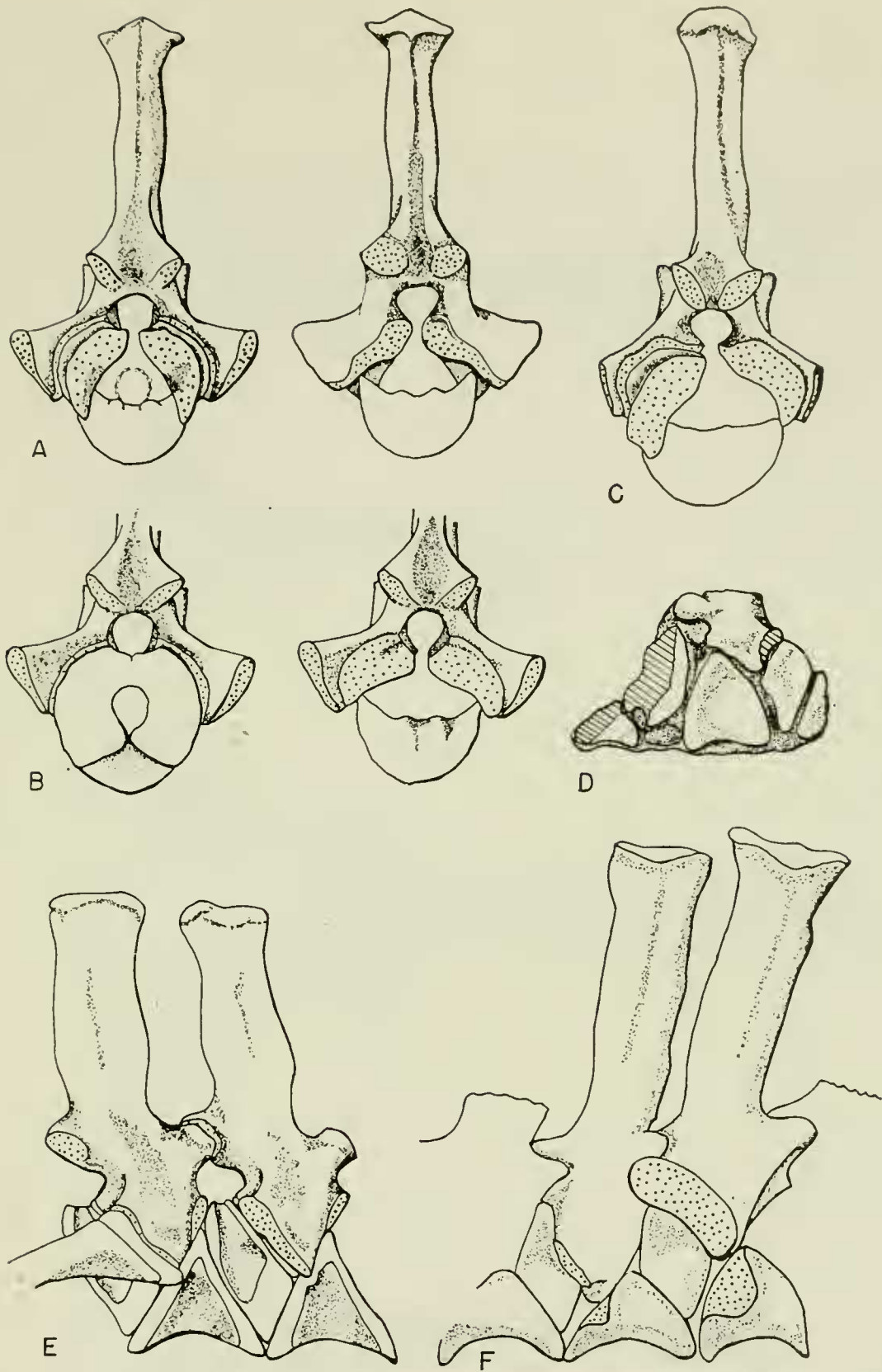
Figure 10. All × .5. (A) *Eryops* vertebra 13, posterior (l.) showing position of notochord and anterior views. (B) *Eryops* vertebra 13, posterior views, with (l.) and without reconstructed cartilages surrounding bony centra. (C) *Eryops* vertebra 21, posterior view. (D) MCZ 1828, left view, showing matrix (dark stippling) occupying position postulated for cartilage about centra of presacral vertebrae. (E) Reconstruction of two dorsal vertebrae showing cartilage reconstructed about centra and rib head. (F) *Eryops* vertebrae 23 and 24, right view, showing facets for rib articulation (large stippling).

Figure 11. Smaller and larger dorsal and caudal vertebrae in posterior view showing changes in form attributed to growth, × .7.

cotylosaurs, the zygaphophyses are situated close together with but a short interval between the medial surfaces of the components of each pair. The typical dorsal zygapophyses are tilted so that the posterior zygaphophyses face about 45° out from the me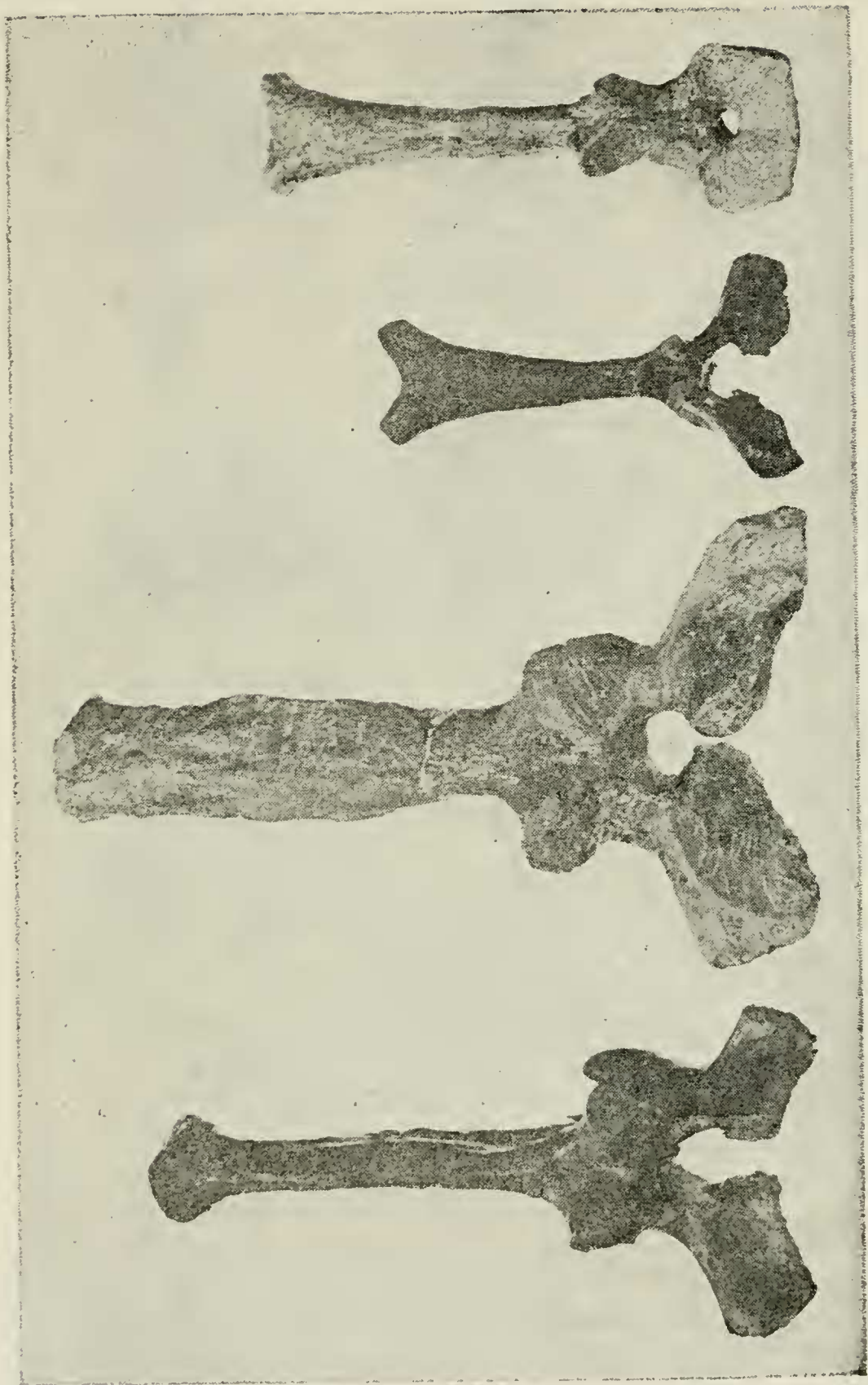dian plane and 45° up from the horizontal plane, and diverge 30° laterally from the median plane; the anterior ones face 45° in, 45° down and diverge 30° laterally. The angles of the zygapophyses vary somewhat throughout the length of the column, the posterior zygapophyses tending to be nearer the horizontal and smaller anteriorly than posteriorly. The face of the posterior zygapophyses is quite flat throughout, the anterior concave.

Continuing to consider a mid-dorsal vertebra, below the level of the zygapophyses the neural arch divides into two pedicels; between them these form a well-defined roof and lateral walls for the neural canal, which is subcircular in outline, as the center of the floor is unossified. The degree of closure of the pedicels below the neural canal, however, is a function of age and size or both (Fig. 11). One can demonstrate sacra (MCZ 2604, 4305) and a caudal vertebra (MCZ 3316, Fig. 11) with a completely ossified neural canal, and a whole series of dorsal vertebrae in which it is nearly closed ventrally (MCZ 3316, Fig. 11). Where the floor is unossified, cartilage probably formed a ventral apex to the neural arch between intercentrum and pleurocentrum in life.

Laterally, the surface between the anterior and posterior zygapophyses is smooth, but there is a depression, usually rather shallow, behind and below anterior zygapophysis. At about the midpoint of the length of this depression a ridge develops that swings down and back into the dorsal edge of the transverse process, presumably associated with the passage of a segmental blood vessel.

The anterior and posterior margins of adjacent vertebrae, below the zygapophyses, form the posterior and anterior margins respectively for the intervertebral gaps that afforded exit for the spinal nerves. These margins do not, however, form ventral boundaries for the gaps.

The posterior surface of the neural arch on each side, from the level of the neural canal floor down over the pedicel, includes a very large unfinished area which faces as much inward and downward as backward. It is subquadrate in form, but rounded in the dorsolateral margin. This surface corresponds

to that on the anterior surface of the pleurocentrum and is articulated with the anterior face of that element, although obviously with an intervening thickness of cartilage. The roughened anterior face of the pedicel, continuous with the posterior face at the ventral edge, is much smaller and irregularly shaped. The upper portion, adjacent to the spinal canal, is subcircular with a pronounced convex mass of bone projecting backward and inward. The more ventral portion of this surface slants downward and outward, narrowing rapidly, becoming concave rather than convex, and twisting so as to face a little inward. This surface matches the posterior face of the next anterior pleurocentrum to a moderate degree and undoubtedly apposed it; there must have been a considerable thickness of cartilage between the two.

The transverse process is rather variably developed. It is typically wedge-shaped in section and at the distal articular surface broad above, narrower below. Typically, the dorsal margin arises in a ridge projecting laterally beyond the surface of the arch pedicel. It faces backward and downward so that the articular surface in a mid-dorsal vertebra faces back about 40° and about 30° downward, in anterior vertebrae more directly laterally.

In a mid-dorsal, the articular surface for the rib extends downward to form the most ventral part of the arch ossified; typical anterior vertebrae are similar. Posteriorly the articular area becomes reduced to the dorsal part of the articulation. In more anterior dorsals, there are two distinct portions: (1) a broader oval dorsal area meeting the tubercle; (2) a thinner ventral extension. Posteriorly, the ventral part disappears and the upper part becomes thin; anteriorly the upper part remains thick and the ventral part tends to thicken as well, until the articular surface becomes a unit.

The measurements of *Eryops* dorsal vertebrae presented in Table 1 are based on AMNH 4280, which includes a set of dorsal vertebrae to which definite numbers can be assigned, and MCZ 1539, the mounted specimen. From the information provided by these two specimens, it has been possible to estimate the position of isolated *Eryops* presacral vertebrae through the size ranges most abundant in collections I have studied. Measurements of isolated *Eryops* vertebrae have been published by Cope (1877, 1878a,b) and Case (1911).

Table 1. Some Measurements of *Eryops* Dorsal Vertebrae

Vertebra number	Length of rib articular facet on transverse process (AMNH 4280)	Inclination from vertical of rib articular facet (AMNH 4280)	Greatest width of articular facet (AMNH 4280)	Height of neural spine above angle with anterior zygapophysis (MCZ 1539)	Distance from atop rib articulation to top of neural spine (MCZ 1539)	Greatest length of vertebra at zygapophysis tips (MCZ 1539)
1	—	—	—	—	—	—
2	—	20°	8 mm	—	59 mm	—
3	—	15°	8 mm	50 mm	70 mm	—
4	—	20°	16 mm	c. 30 mm	c. 53 mm	31 mm
5	—	10°	14 mm	55 mm	70 mm	35 mm
6	—	10°	12 mm	58 mm	70 mm	36 mm
7	30 mm	35°	11 mm	58 mm	70 mm	40 mm
8	33 mm	35°	—	59 mm	75 mm	41 mm
9	—	40°	10 mm	62 mm	75 mm	43 mm
10	30 mm	45°	—	62 mm	77 mm	39 mm
11	30 mm	40°	8 mm	64 mm	78 mm	41 mm
12	28 mm	40°	—	62 mm	78 mm	41 mm
13	25 mm	35°	7 mm	63 mm	78 mm	40 mm
14	25 mm	30°	—	64 mm	79 mm	45 mm
15	20 mm	25°	6 mm	65 mm	84 mm	43 mm
16	20 mm	30°	—	68 mm	88 mm	42 mm
17	20 mm	30°	4 mm	70 mm	91 mm	45 mm
18	20 mm	35°	—	70 mm	91 mm	42 mm
19	—	—	—	72 mm	94 mm	40 mm
20	—	—	—	74 mm	95 mm	44 mm
21	—	—	—	73 mm	93 mm	41 mm
22	—	—	—	74 mm	100 mm	41 mm
23	—	—	—	75 mm	100 mm	40 mm

THE INTERCENTRA OF PRESACRAL VERTEBRAE
(Figs. 1–4; 9 I; 10; 12; 13 A–C)

The dorsal intercentra are of the usual rhachitomous type, being crescents as seen in anterior and posterior view, convex side down. They are wedge-shaped in side view, apex upward. Concavities on their external surfaces may mark the paths of blood vessels. The inferior surfaces tend to descend as flanges anteriorly and posteriorly, least so in the posterior dorsals. A flat longitudinal ridge tends to develop mid-ventrally, best seen in the dorsal region. The surface may be notched posteriorly at the area of rib capitulum articulation. This is not well seen in young individuals and may be lacking in fairly large animals. It is most emphasized anteriorly in the presacral column, and at the sacrum (Fig. 12).

The anterior, posterior and dorsal surfaces are rough and unfinished, and presumably were continued in cartilage. The dorsal notch is a rounded longitudinal depression, occupied in life by the notochord and surrounding tissues. Four hummocks of bone, two fore and two aft, are arranged on either side of the depression and may represent centers of ossification (Fig. 13 A). These hummocks show with varying clarity, sometimes are completely obscured, and are illustrated as ridges by Broili (1899). Seen in side view the anterior pair of hummocks is slightly more ventral than the posterior in dorsal intercentra; the posterior hummocks are closer to the top of the intercentra.

Cartilage, with which the intercentrum was continuous, may have surrounded the notochord in life (Romer, 1947), but no ring intercentra have been found. Coossification of the pleurocentra occurs below the neural canal (Fig. 13 E), above the notochord (MCZ 2622 and 1652). Such a coossified piece may in turn coossify with the intercentrum to form a type of ring centrum in which all three elements are distinguishable (MCZ 2604 and 2562). A completely coossified vertebra has also been studied (FMNH UR745). Such remains are perhaps the best evidence of a vertebral column of ossified pieces embedded in a matrix of cartilage in *Eryops*.

Intercentra that were broken during life are rarely found. Two dorsal intercentra have been found (MCZ 2621, 4306; Fig. 13 B, C), which I think were so broken; a third (MCZ 4305) is cracked diagonally on the dorsal surface. Each break is at an angle clockwise to the anteroposterior axis (2621, 8°; 4306, 30°;
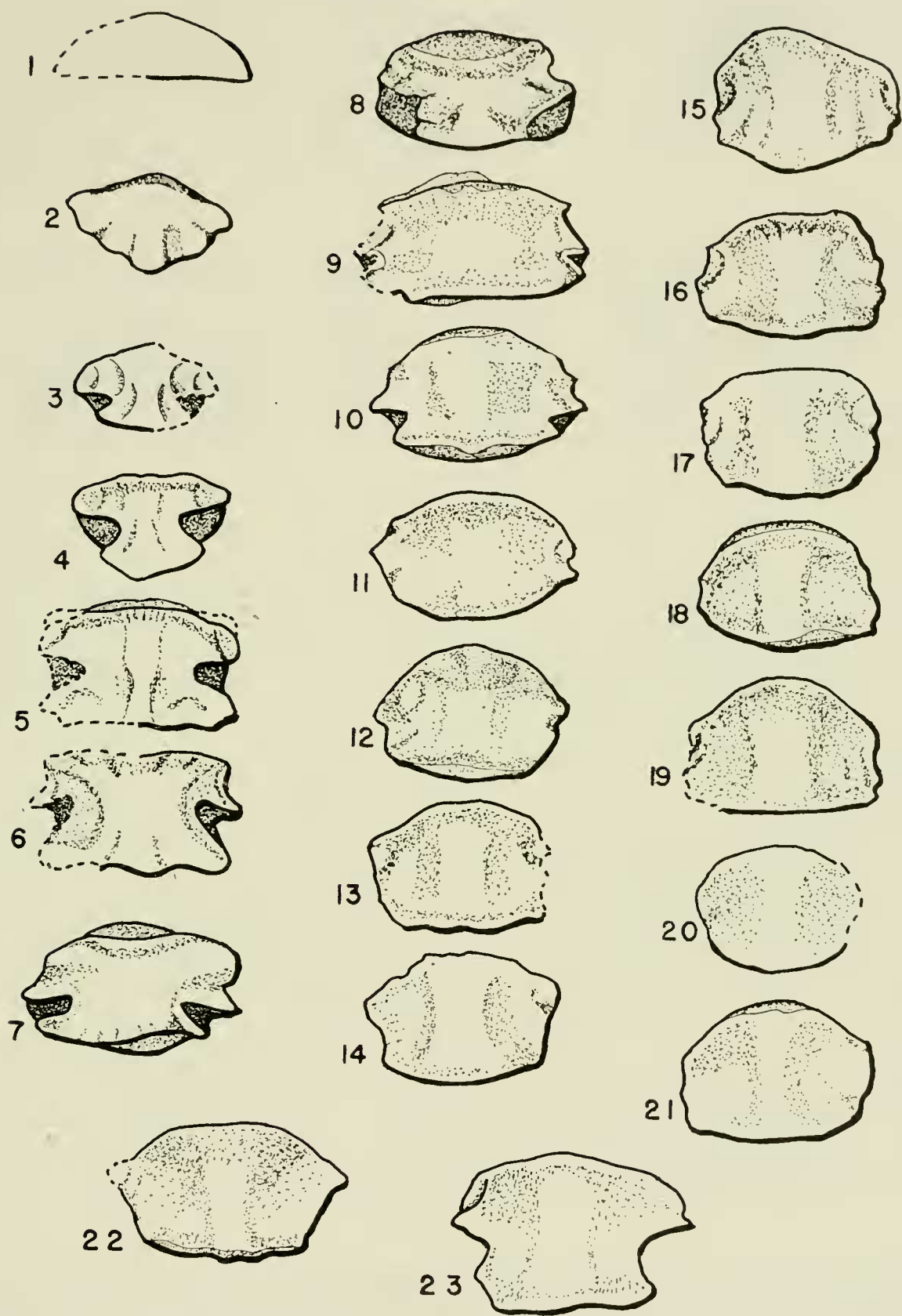
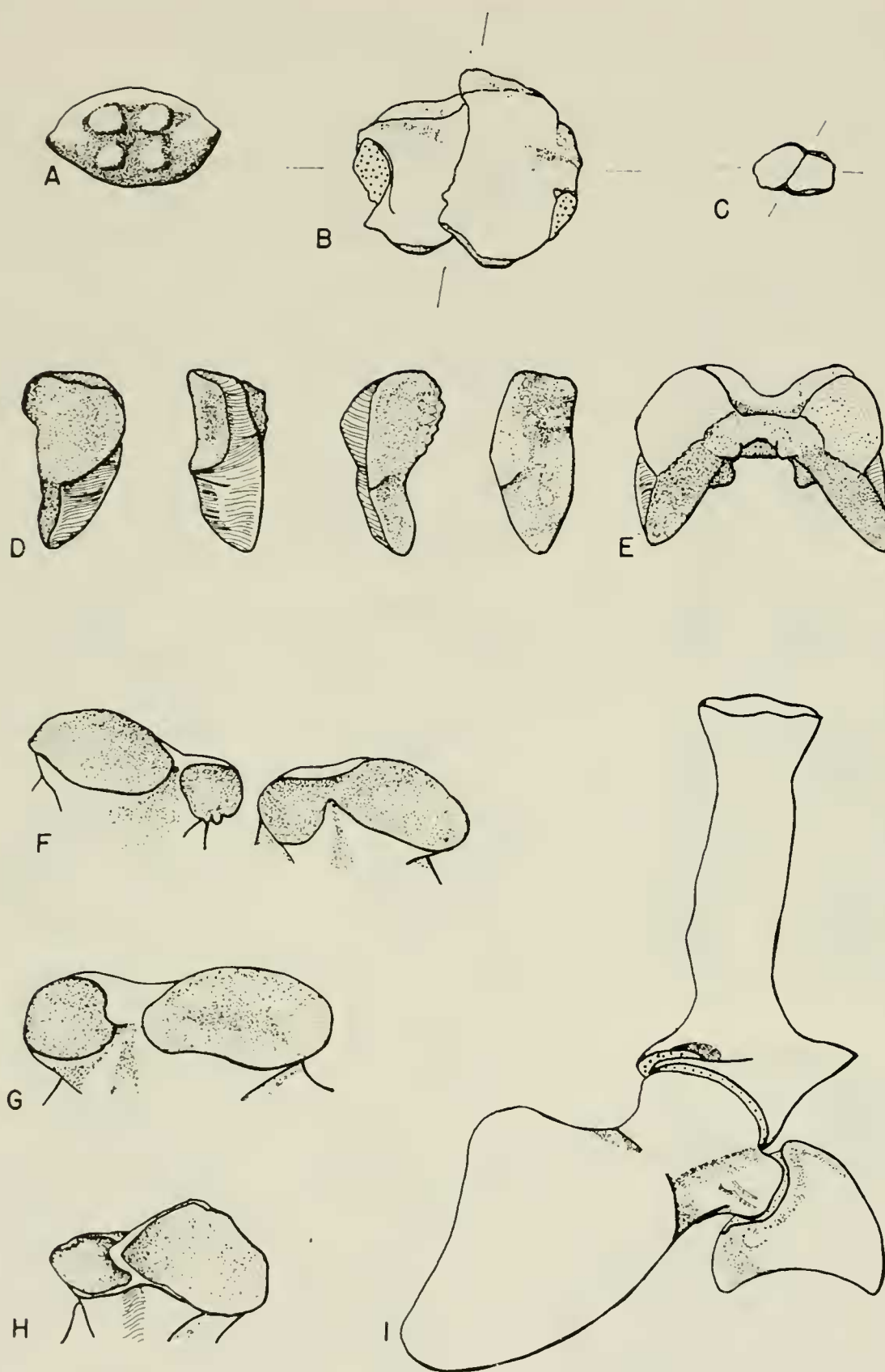Figure 12. The presacral and sacral (23) intercentra of *Eryops* in ventral view, anterior uppermost, × .6.

Figure 13. All × .5. (A) *Eryops* presacral intercentrum showing paired protuberances, anterior uppermost. (B) MCZ 2621, presacral intercentrum, ventral view, anterior at top, showing inclination of healed break. (C) MCZ 4306, intercentrum, as in (B). (D) MCZ 4307, a left pleurocentrum in anterior, lateral, posterior and medial views. (E) MCZ 2591, anterior view of coossified pleurocentra. (F) MCZ 4325, left and right sacral rib central articulations in ventromedial views. (G) MCZ 2085, right sacral rib central articulations in ventromedial view. (H) MCZ 2621, right sacral rib central articulations in ventromedial views. (I) Sacral vertebra and right sacral rib of *Eryops*, right view, pleurocentra not shown.

4305, 30°). That these breaks occurred in younger animals is evidenced by the small size of one intercentrum (MCZ 4306) and the appearance of extensive growth after healing in the other (MCZ 2621).

A fragment of the atlas intercentrum still clings to the left element of the atlas in AMNH 4183 (omitted by Cope and Matthew, 1915: pl. 12).

THE PLEUROCENTRA OF PRESACRAL VERTEBRAE
(Figs. 1–4; 9 I; 10; 13 D, E)

The pleurocentra are paired ossifications, the centers for which are situated dorsal to the notochord rather close to the midline. Study of articulations of components of the vertebrae indicate, however, that they must have been situated in pleurocentral cartilages of much larger size. Such cartilages would have appeared rhomboidal in side view, their longer sides articulating anterodorsally with the arch of the same vertebra, anteroventrally with their own intercentrum, posterodorsally with the next posterior neural arch, and posteroventrally with the next posterior intercentrum.

Their contours indicate that the ossified pleurocentral elements came close to the ventral margin of the column but did not reach it externally; restoration of the cartilage suggests that the cartilaginous pleurocentra probably did not gain contact with each other ventrally (Fig. 10 B). Dorsally, however, they were obviously in broad contact beneath the spinal cord; occasional coossifications in old specimens would suggest that the cartilages may have been continuous below the floor of the neural canal. The conjoined elements would have given in end view the appearance of an inverted crescent with the two horns closely approximated ventrally. The cartilaginous pleurocentra could have closely approximated those seen in ossified form in *Trimerorhachis*.

The paired centers of ossification of the pleurocentra appear to have been situated far dorsally where there is a globular mass of bone from which ossification proceeded slowly toward the ventral part of the element. The pleurocentra appear to be feebly ossified, and much of their surface area is unfinished in all but very old specimens. The more anterior pleurocentra are in general less ossified, and far anterior ones are almost unknown (see also Branson, 1905). A fifth pleurocentrum in the MCZ

mount is finished on almost none of its surface, a fourth is a tiny nubbin on one side only and coossified with the arch, and there are no traces in material known to me of pleurocentra 1 and 2.

Exceptionally the two pleurocentra may abut medially, as they do in sacral vertebrae in two mature specimens (MCZ 2669 and 4305). There are cases in which the pleurocentrum has coossified with the neural arch, as on one side in two different sacra (MCZ 4305, 2604), and cases of coossification with the intercentrum behind (FMNH 60), or at one level with intercentrum and at another with neural arch (MCZ 1387), or with both in the same vertebra (FMNH UR745). Such cases are suggestive of a continuum of cartilage, the vertebral pieces embedded in it, similar to what Parrington has proposed.

The pleurocentra are likely to abut in the caudal region (MCZ 1787 and 2634), even to the point of occluding the notochordal canal (Fig. 15 F). The anterodorsal face of a pleurocentrum, that which articulates with the neural arch of its vertebra, is nearly flat and forms essentially a quadrant of a circle with a curved margin laterally and ventrally. In life this surface faced somewhat up and out as well as anterior and was apposed to the neural arch, although separated by at least a film of cartilage from it. The posterior surface is irregular, convex above, and apposed to but rather far from the anterior margin of the neural arch. The medial and posterior surfaces present a continuous, rough, curving form.

The external surface is in great measure finished. It is wedge-shaped in external view, narrow above, broadening and then tapering below. The margins curve up sharply anteriorly and posteriorly so that the pleurocentrum is externally concave in section; the curved margins are best defined above. The groove between the margins conveyed a spinal nerve. It narrows dorsally and at the very top turns anteriorly above the anterior articular surface to blend smoothly into the lower wall of the neural canal. The constant mismatch between the large surfaces on the neural arches for articulation with pleurocentra and corresponding anterior articular facets of the pleurocentra collected at the same time and place is a measure of the extent of cartilage beyond the borders of the ossified pleurocentra.

THE ATLAS–AXIS COMPLEX
(Figs. 1; 9 A–G; 14; Pl. I)

The neural arch of the atlas is highly specialized. The two

sides may be separate (MCZ 1883) or coossified (AMNH 4183; Case, 1911). In the former case, each side consists of a stout pedicel and slender half arch and neural spine directed dorsoposteriorly. The pedicel is wedge-shaped with two broad articular surfaces, anteroventral and posteroventral. The anterior surface is for articulation with an exoccipital; the posterior is finished above (MCZ 1883), rough below where it articulated with the intercentrum of the axis. Each articular surface is a quadrant of a circle with a common straight ventral margin. The posterior surface is somewhat concave, not flat as usual. Internally there is a well-marked curved area for the side wall of the neural canal. At the base of the spine on each side is a flat tubercle, a well-defined anterior zygapophysis to seat the proatlas. Each half-spine is a thin rod, posteriorly and dorsally directed close to the axis spine. A tubercle or slight flange on the lower edge of the half-spine rested in life on the corresponding anterior zygapophysis of the axis.

The atlas intercentrum, seldom preserved, appears to ossify late. That associated with Sawin's (1941) specimen is a very flat crescent, with the outline of a slight notochordal space above, and the anterior edge with a central depression. There is only one pair of mounds, and the back surface is unexceptional. The front is subdivided into two articular areas facing rather laterally as well as anterodorsally, and obviously covered with much cartilage in life. The intercentra of atlas and axis have no capitular facets.

Each proatlas is a small neural arch, the short neural spine slanting back and upwards, its tip being irregularly rugose. At its base is an articular facet for the atlas tubercle. The anterior limb defines the upper edge of the foramen for the first spinal nerve and appears to barely touch the exoccipital region of the skull above and lateral to the foramen magnum; there is no formed facet.

There was undoubtedly restricted motion of the head, in the absence of a neck; the atlas-skull joint probably acted as a dorsoventral hinge.

The axis neural arch is in many respects an ordinary one (Fig. 10). The neural spine is however elongated anteroposteriorly. The spine slants backward and then angles up in its longer dorsal portion, relative to a plane through the zygapophyses. The spine is wedge-shaped in frontal section, and is generally thicker posteriorly than anteriorly. There is a variable but gen-
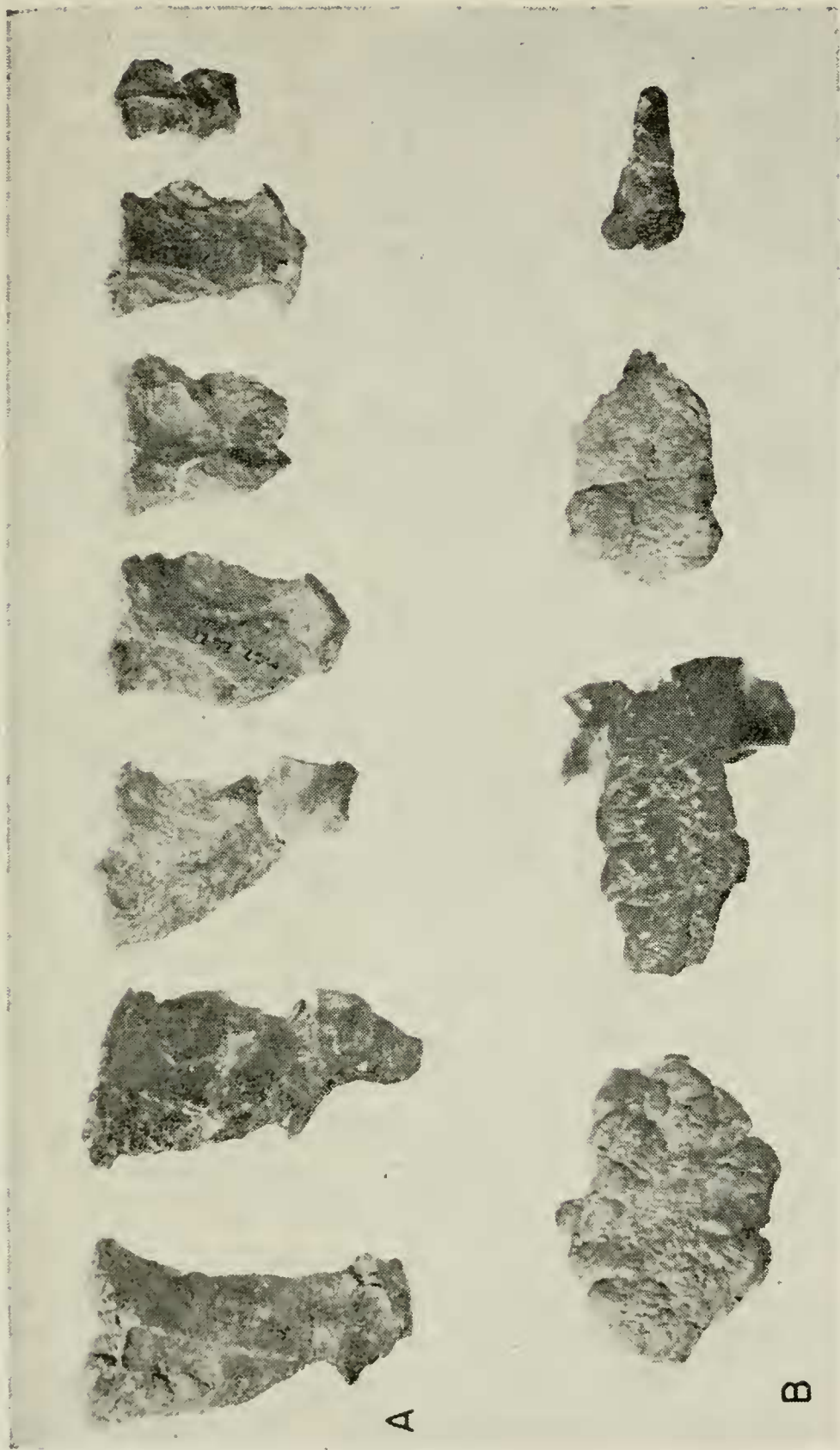
Figure 14. (A) Axis spines of *Eryops* cf. megacephalus, right lateral view. Left to right MCZ 2621, 1883, 3241, 2621, 3258, 4303; CMNH 11025 (*E. avinoffi*), × 5. (B) Dermal ornamentation of *Eryops* axial spines, anterior to right, dorsal views. L. to r. MCZ 2621, 1883, 2621; CMNH 11025, × .7.

erally prominent angle posteriorly, toward which a ridge is directed on either side from the widest point of the dorsal surface. Development at the front of the neural spine is very variable, depending in part on preservation. It is likely that a well-developed thin flange occurred on the front of the axis spine for a median ligament to the occiput. The anterior zygapophyses are much reduced to small flattened areas for articulation with the arch of the atlas. The pedicel and transverse processes are not specialized. The intercentrum of the axis is flat-bottomed, broad, and the posterior end has a rounded projecting keel. The axis is the most anterior vertebra to bear a rib. Constancy of form of the axis spine is illustrated in Figure 14 A.

VERTEBRA FOUR
(Figs. 1; 9 H; Pl. I)

This vertebra, with its specialized neural spine and anterior zygapophyses, makes up for restrictions in movement at the occiput. The posterior zygapophyses are normal, but the anterior ones are greatly expanded and nearly horizontal, thus permitting freedom of motion in the horizontal plane, together with some rotation vertically. The spine is much reduced (Case, 1911; Romer, 1943), a fact apparently not revealed by Cope's material. The spines of vertebrae 3 and 5 are inclined toward each other above that of 4; they are therefore distinctive. Their neural spines like that of the axis are somewhat elongate anteroposteriorly, and their facing edges are thinned, suggesting a special connection taking up the movement between vertebrae 3 and 4. These features are illustrated in Figure 1. In the Field Museum mount the spine of vertebra 4 curves slightly forward.

THE SACRUM
(Figs. 4; 10 F; 15 A; 12; 13 F–I)

The spine of the sacral vertebra is high and slants backward; in the MCZ mount the highest spine is that of vertebra 26, three behind the sacral (Table 2). The anterior zygapophyses are quite large, being the most posterior of an increasing size series. The posterior zygapophyses comprise approximately half the area of the anterior. The transverse process is enormously developed for articulation with the large tuberculum of the sacral rib, and the intercentrum bears a large facet for the capitulum. The facet may impinge upon the pleurocentrum (Fig. 15 A; FMNH
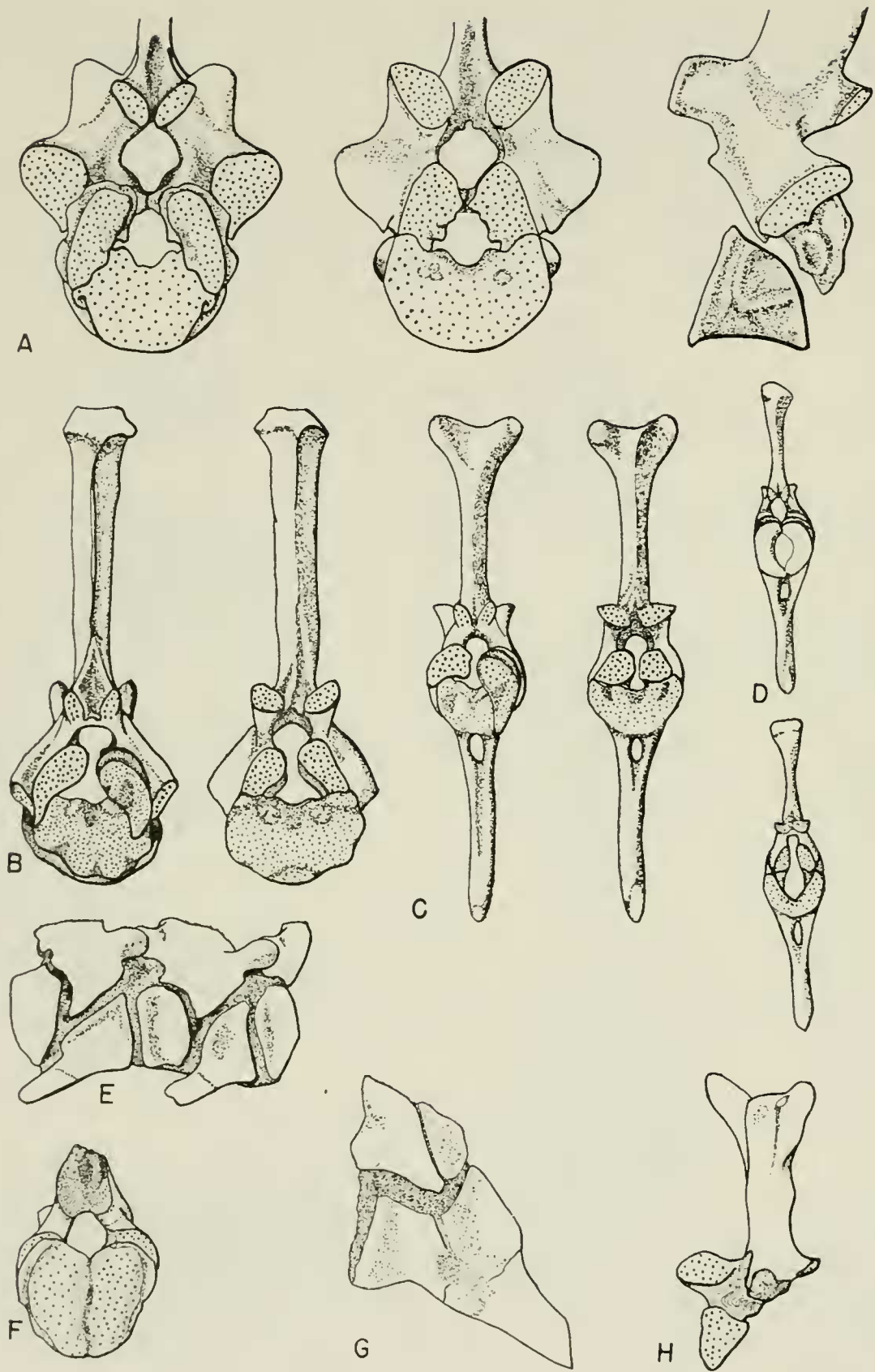
Table 2.   Some measurements of *Eryops* Anterior Caudal Vertebrae
(MCZ 1539)

Vertebra	Height of Neural Spine	Greatest Length of Vertebra
1	75 mm	35 mm
2	78 mm	35 mm
3	80 mm	35 mm
4	73 mm	38 mm
5	71 mm	—
6	65 mm	36 mm
7	59 mm	—
8	59 mm	35 mm
9	52 mm	—
10	51 mm	35 mm
11	47 mm	31 mm
12	41 mm	31 mm
13	44 mm	—
14	38 mm	—
15	36 mm	29 mm
16	40 mm	—
17	39 mm	—
18	40 mm	—
19	33 mm	26 mm
20	33 mm	—

←

Figure 15.   All × .5.   (A) *Eryops* sacral vertebra (23), spine omitted, in posterior (1.), anterior and left views, the latter of MCZ 4305.   (B) *Eryops* vertebra 27 (caudal 4), posterior (1.) and anterior views.   (C) *Eryops* vertebra 33 (caudal 10), posterior (1.) and anterior views.   (D) *Eryops* vertebra 43 (caudal 20), posterior (above) and anterior views.   (E) MCZ 2634, right view, showing matrix (dark stippling) occupying position postulated for cartilage about centra of postsacral vetebrae.   (F) MCZ 1787, posterior view, spine missing, showing closure of notochordal canal by pleurocentra.   (G) AMNH 4183, left view, showing fusion of two successive chevrons.   (H) MCZ 4325, left lateroanterior view of one to three caudal vertebrae showing perforation of dorsal expansion of neural spine on the left side for segmental blood vessel.

UC60 and UC117), this being a characteristic of old and of
very large specimens. The sacral rib may fuse to or coossify
with its central articulations (FMNH UC117). The coossifica-
tion of elements is not uncommon at the sacral vertebra, al-
though the degree of fusion may differ on the two sides (MCZ
4305, 2669, 2604).

THE CAUDAL VERTEBRAE
(Figs. 5–8; 15 B–H; 11; the measurements in Table 2)

The total number of caudal vertebrae in *Eryops* is about 40.
The number of vertebrae may vary, but the possession of ribs on
the first eight caudals with chevrons beginning on the eighth
vertebra is taken as typical. The proximal caudal neural arches
are closely comparable to the presacral ones in their general fea-
tures, with less anteroposterior extension at the top, and with the
zygapophyses placed more closely together. In the trunk region,
the shaft of the neural spine tends to curve back and then up,
whereas in the caudal the longer part reaches upward before the
backward bend, this curvature being more pronounced pos-
teriorly. The heights of the caudal spines gradually decrease and
the tops change from an oval outline and become bifurcated, at
about caudal 4, into two abbreviated horns with rounded sum-
mits, one on each side, directed first posterolaterally (4–10),
then laterally (11, 12), and then anterolaterally (13–20). Be-
hind caudal 20, bifurcation is not noticeable. The horns are not
always symmetrical; one may be anterior to the other. They
were covered by skin in life (Romer and Witter, 1941). Near
vertebrae 20 to 22, the neural spine tips are altered, becoming
single again. By this point, the spine is much shortened with a
strong back-and-up curve, is thin from side to side, and is rather
long anteroposteriorly.

The zygapophyses are closer together and more sharply tilted
than in the dorsal vertebrae, and there is a reduction in size.
In the first dozen caudals, the sides of the neural arch tend to
be somewhat concave between the zygapophyses, as in the dorsal
vertebrae. After that they are quite flat. In the MCZ mount
transverse processes with broad but thin ends that gradually
narrow occur on the first seven caudals and exceptionally on one
side of the eighth. Behind the eighth, the pedicels are smooth,
although convex and swollen along their posterior borders. Each
vertebra, and hence its pedicels, becomes relatively and increas-
ingly narrow in the tail, so that the sides of the pedicels are more

vertical. The surfaces facing the pleurocentra and intercentrum are similar to those in the trunk for most of the length. In old specimens, the floor of the neural canal may be complete (Fig. 11), suggesting that cartilage extended through the area in younger specimens. The pedicels narrow below the spinal nerve foramina.

In the proximal part of the caudal column, each pleurocentrum tends to broaden at the top, flatten on the lateral surface, and extend relatively far down. They tend to become relatively large and more important, and distally may approach the embolomerous ring type (MCZ 2634). In the sacral region especially, the two bony pleurocentra become closely approximated dorsally, and the ventral ends tend to approach one another more closely than elsewhere. It is possible that in mature specimens they fused into a ring, but no such specimens have been seen, although intercentrum and pleurocentra together may coossify into a ring centrum. Pleurocentrum enlargement and coossification of vertebral elements in the sacral region may be adaptations for terrestrial life.

In the MCZ mount, the first seven intercentra of the tail lack a haemal arch; the first chevron is on the right side of vertebra 8, the left side presenting a transverse process and rib. This count may have varied depending on the extent of the coelom in the cloacal region. The proximal intercentra are like those of the trunk, but capitular facets are well marked and the intercentra are more convex ventrally than dorsal intercentra. A medial ventral groove appears in intercentrum 7 for the caudal blood vessel which posterior to vertebra 7 courses through the foramina of the haemal arches. These arches tend to develop a keel on the front and to be flat behind, and to develop small terminal cartilages. The shafts gradually become shorter, the foramina occupying a progressively greater extent of their length. Distally, the ends become flattened and tend to become antero-posteriorly oriented, shoe-shaped expansions.

To a greater or lesser extent, the neural spines of *Eryops* vertebrae show lateral grooves where segmental blood vessels have coursed. On each of three caudal vertebrae of MCZ 4325, near the front of the bifurcated spine series, a shallow groove appears on the left side of the neural spine perforating or indenting the dorsal tuberosity of the neural spine (Fig. 15 H). These three are unique in the collections I have studied; presumably all came from the same animal.
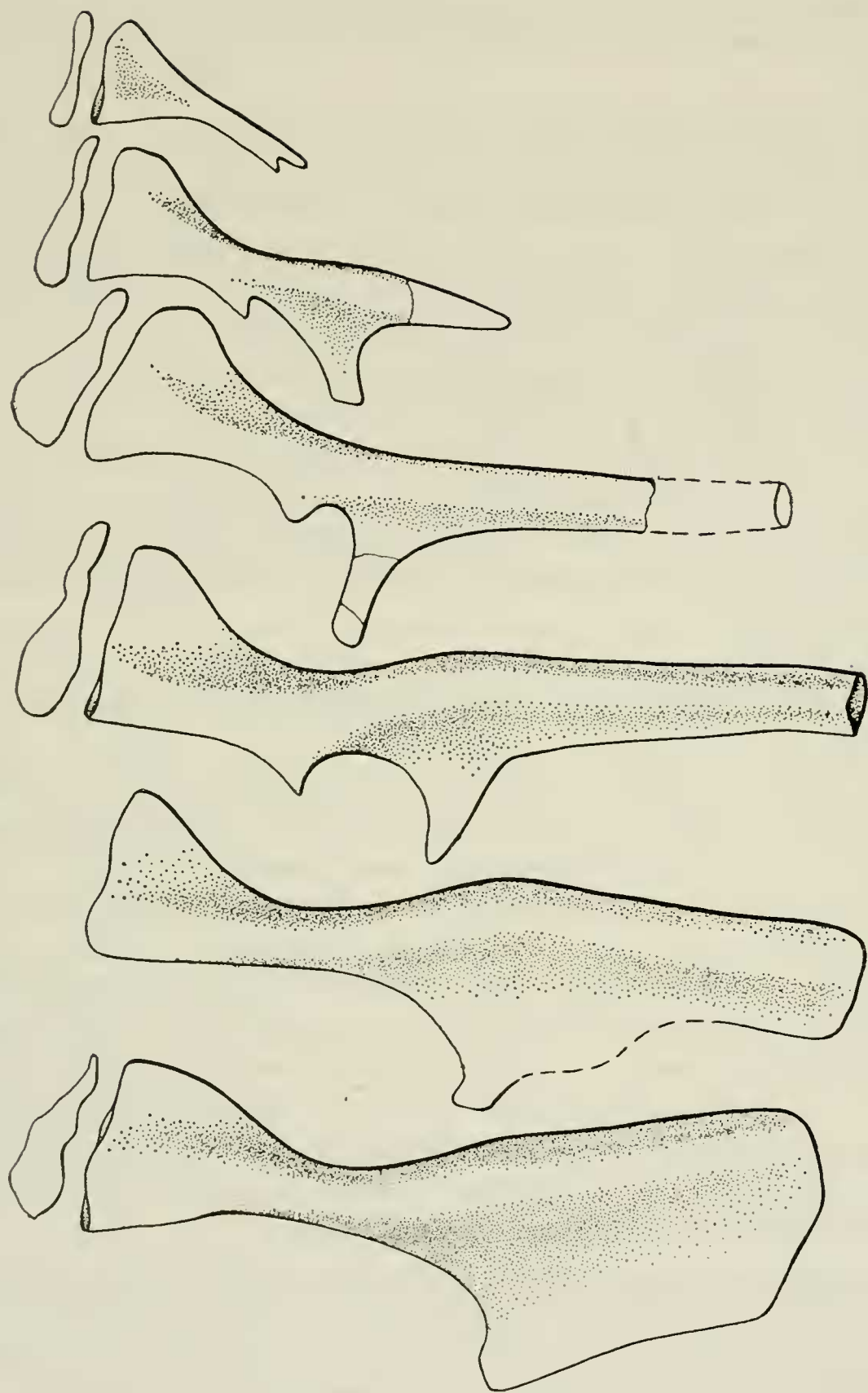
Figure 16. *Eryops* right presacral ribs 1–6 (of vertebrae 2–7) with outlines of articular surfaces above; × .5.

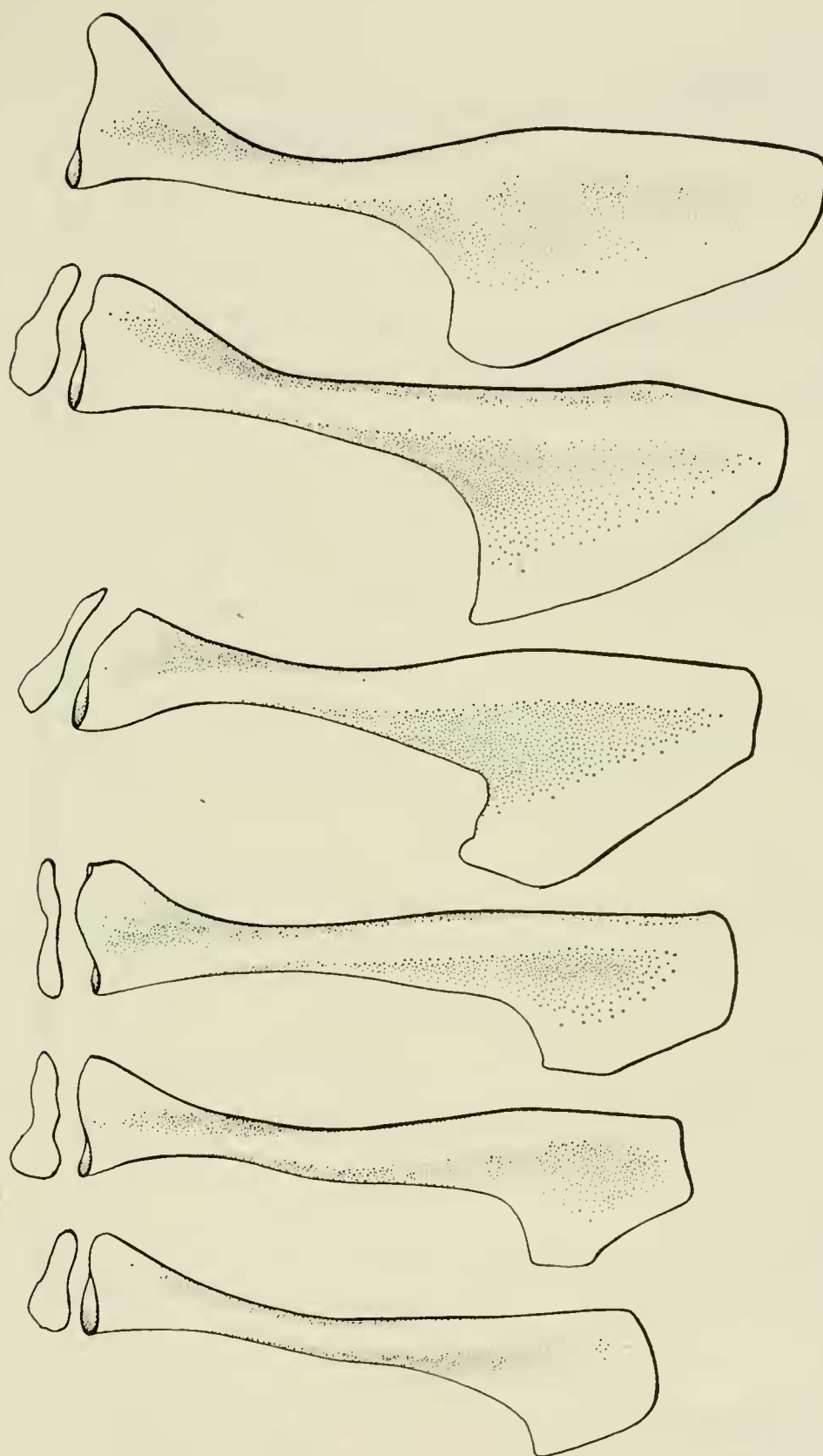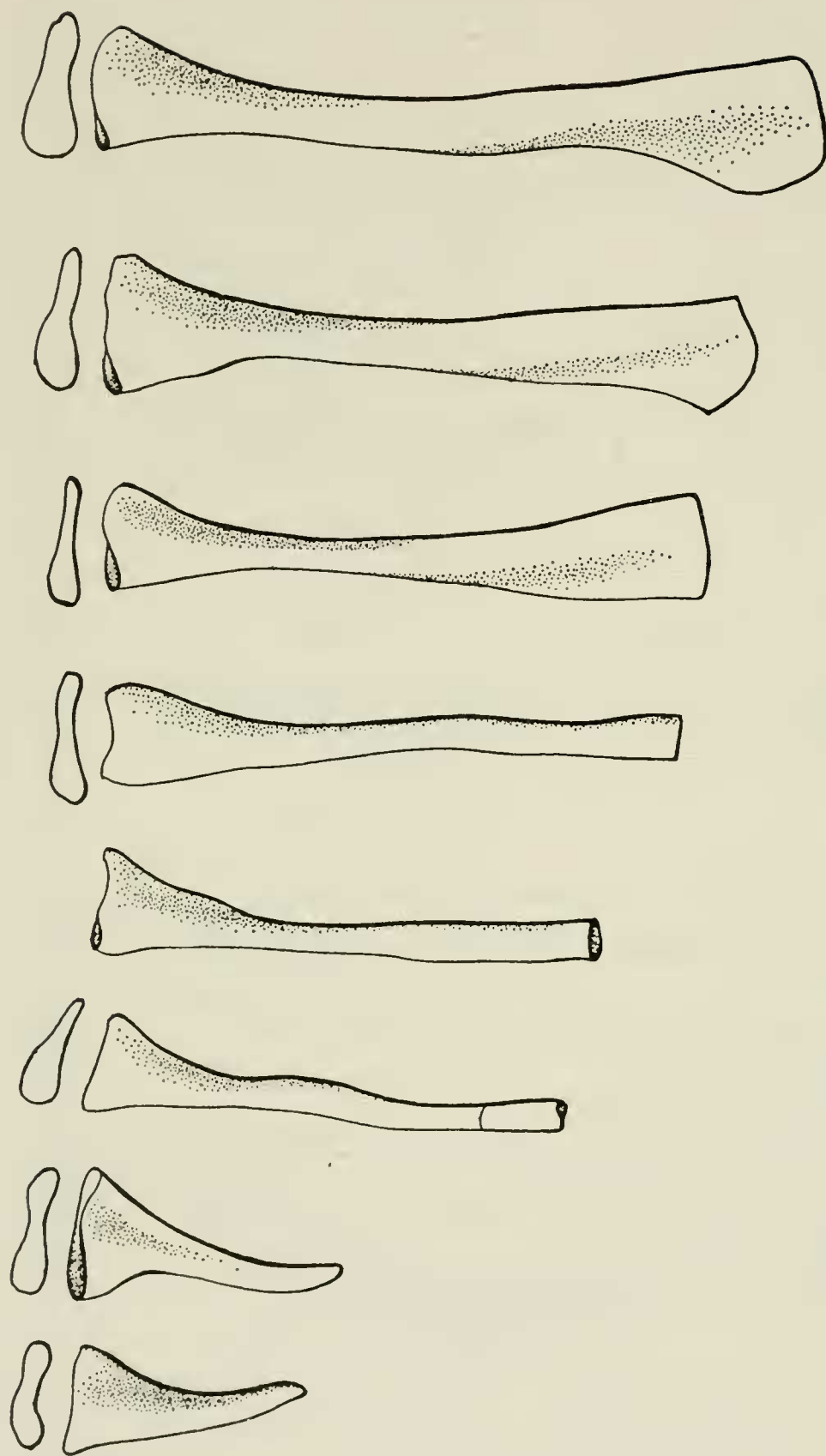Figure 17. *Eryops* right presacral ribs 7–12 (of vertebrae 8–13), × .5.

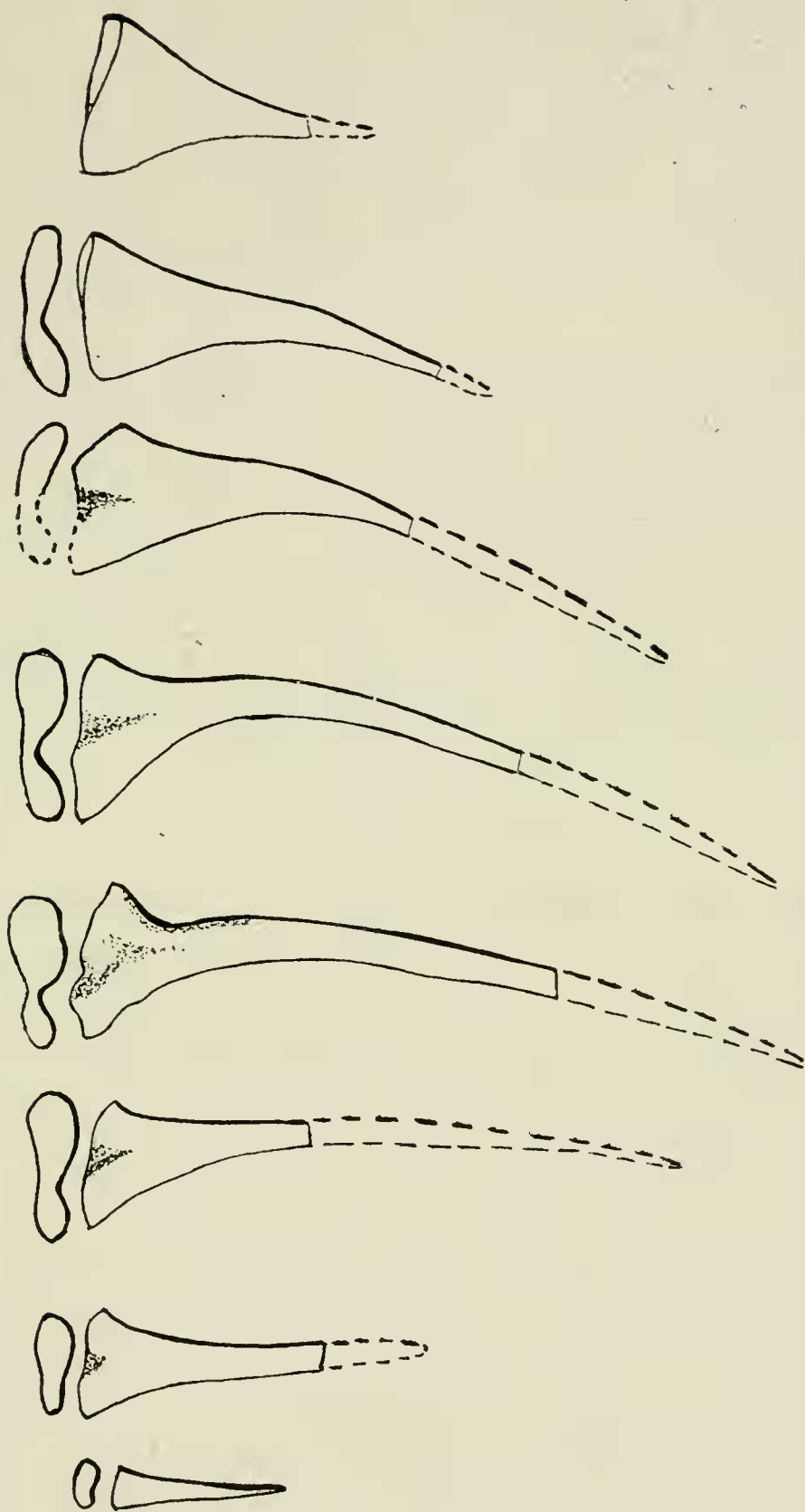Figure 18. *Eryops* right presacral ribs 13–20 (of vertebrae 14–21), × .7.

Figure 19. *Eryops* right postsacral ribs 1–8 (of vertebrae 24–31), × .7.

THE RIBS
(Figs. 13 F–I; 16–19)

Of the 22 presacral vertebrae, the first (atlas) lacks a rib; in some mounts the last presacral rib, that of vertebra 22 has been omitted, while in others a misplaced ilium spans too many ribs.

The head of all presacral ribs is expanded, with only a constriction separating capitulum and tuberculum. The tubercular part is somewhat thicker than the capitular. The articular surfaces are somewhat concave and unfinished, suggesting a cartilaginous surface coat. The proximal rib ends are inclined clockwise from the vertical, as are the corresponding articular surfaces of the transverse processes (Table 1). The ribs are flat distally.

There are thickenings of the shaft continuous with capitulum and tuberculum, and there may have been considerable variation in the form of the uncinate processes. The distal rib ends are unfinished, except those of the posterior presacrals, and presumably ended in cartilage, but this is uncertain. In the MCZ mount, uncinate processes are shown on the 2nd through the 13th ribs, reducing in size and disappearing as the ribs shorten posteriorly. Caudal ribs lack these structures.

DISCUSSION

It is clear that — distortion apart — individuals of *Eryops* were variable in the following details of their spinal columns: extra processes and exostoses; closure of neural canal; degree of definition of capitular facets; relative sizes of neural arches, intercentra and pleurocentra; degree and asymmetry of coossification; shapes of neural spines and of atlas, axis and the special fourth vertebra; angles of inclination of the neural spines, and details of configuration of their dorsal expansions. Nevertheless, a clear picture emerges of a repeated series of ventral intercentra, dorsal neural arches and paired dorsolateral pleurocentra probably separated or held together in life by cartilage, which may have been continuously woven among the centra or interrupted between vertebrae anterior to each intercentrum; it is not clear from the fossil record which was the case. Presumably cartilage was more extensive in younger than in older animals. The unfinished articular surfaces of vertebral elements clearly reflect their continuation in cartilage.

Arrangement of vertebral elements varies considerably in existing *Eryops* reconstructions. Fossilized pieces, even when found

adjacent, are, unless coossified, often difficult to fit exactly to each other, presumably due to the missing cartilage. We have found no reason to quarrel with Cope's (1890) description, which is an excellent guide to vertebral arrangement in *Eryops:* "The neural arch rests exclusively on the pleurocentrum, which in turn adheres to the intercentrum behind it by its long side, and to that in front by its short side or end", and of caudal vertebrae ". . . the pleurocentra descend further than in the dorsal region, rarely to the inferior face of the column, and separating the intercentra from mutual contact." These points are illustrated in Figures 10 and 15.

As regards the function of the rhachitomous vertebral column, two views have been advanced. Cope (1884) proposed a coat sleeve on a semiflexed arm as a model of the flexible cylinder to which he earlier (1883) had likened the column of *Eryops.* He saw the osseous elements of the rhachitomous vertebral column distributed through a sheath of softer tissue around the notochord, like segments of the skin of an orange — segments of a sphere, as it were. "If you take a flexible cylinder, and cover it with a more or less inflexible skin or sheath, and bend that cylinder sidewise, you of course will find that the fractures of that part of the surface will take place along the line of the shortest curve, which is on the side; and, as a matter of fact, you have breaks of very much the character of the segments of the Permian batrachia" (1883: 276). In a coat sleeve covering the semiflexed arm, the folds represented to Cope the fractures in the flexible cylinder, the intervals between elements, and the spaces between folds the elements themselves. Cope left it to future investigations to determine the applicability of his model to the history of the vertebral column (1884: 32).

Parrington (1967) suggested a geodetic spiral, presenting the rhachitomous vertebral column as a series of discrete ossicles in a cartilage continuum, allowed to twist by virtue of the embedding of the rather rhomboidal osseous elements interdigitated in a cartilage matrix. Such twisting, Parrington suggested, would have been essential for amphibious tetrapods like labyrinthodonts on coming ashore in order to maintain a center of gravity upon a triangle of three legs while bringing the fourth leg forward for the next step. Coalescence of neural arches and neural spines in certain armored rhachitomes has led Vaughn (1971) to question whether or not Parrington's model can have applied to locomotion in these particular labyrinthodonts. On the other hand, the

flexibility in vertebral column which Parrington's model provides would, it seems to me, lend itself ideally to the stereotyped locomotion probably imposed upon a large, tailed amphibian such as *Eryops* by extension of the supracoracoideus muscle, between coracoid and humerus, to the forearm through the coraco-radialis proprius, as I have discussed it for living urodeles (Moulton, 1952). While the arrangement may have relieved *Eryops* from decisions leading to more complicated locomotory patterns, the simultaneous adduction of the forelimb and flexing of the forearm, re-establishing at each step the triangle of three legs as envisoned by Parrington, would have abetted the twisting of a spirally organized vertebral column and vice-versa. It is noted that Miner (1925) questions the occurrence of the coraco-radialis proprius in *Eryops*. Thomson and Bossy have argued (1970) that the temnospondyl and anthrocosaur amphibian lineages represented different experiments in a terrestrial vertebral column, both based on the principle of a geodetic spiral enunciated by Parrington.

The spiral pattern suggested by Parrington seems reasonable as a device for strengthening a vertebral column like that of *Eryops* subject to the stresses of locomotion on land. Are there evidences of the proposed torsion in fossil material? I believe so. Two intercentra broken and healed during life (MCZ 2621, 4306), and one that developed a shallow dorsal split also during life (MCZ 4305) have been encountered (p. 22). Inasmuch as each occurred at an angle clockwise from the primary axis (MCZ 2621, 8°; 4306, 30°; 4305, 30°), I suggest that these breaks may have occurred in young animals and that they may reflect the twisting hypothesized by Parrington in his spiral model. Such breaks are not common in fossil collections, the ones described being unique among the intercentra I have studied.

At present, the detailed pattern of evolution of vertebral centra is unsettled. Recent papers of special significance are those of Williams (1959), Panchen (1967), Thomson and Vaughn (1968) and Thomson and Bossy (1970). Despite gaps in our knowledge of the details, there is a general concensus that some form of the rhachitomous vertebra was the primitive amphibian type; however, increasing evidences of variation in vertebral pattern among primitive amphibians greatly complicate the picture (R. L. Carroll, personal communication). *Eryops* itself has moved along the temnospondylous line from the most primitive labyrinthodont condition (Romer, 1947). In suggesting that the

amphibian centrum is homologous throughout, but differently subdivided in different lineages, Panchen (1967) introduced an idea open to examination by determining the attachments of myosepta to the vertebrae, for in all tetrapods, it is clear since the important review by Williams (1959), caudal and cranial half sclerotomes of successive somites unite, resulting in alternation of vertebrae and primary muscle segments. Panchen saw the vertebral margin of the myoseptum with its segmental blood vessel providing the dividing line between intercentrum and pleurocentrum. In temnospondyls he saw the myoseptum moving posterodorsally, ultimately to the stereospondyl condition, leaving an increasingly large intercentrum ahead of the myoseptum until the pleurocentrum disappeared. Anteroventral movement of the myoseptum on the anthrocosaur line would have resulted ultimately in the loss of the intercentrum, and in an amniote centrum formed from the pleurocentrum posterior to the myoseptum.

While I have no new evidence on the course of the intersegmental blood vessels in relation to the centra in labyrinthodonts, the pathway for the blood vessels and myosepta postulated by Panchen (1967: 28) as applicable to fossil material is supported by the three neural arches of caudal vertebrae (p. 33) which are grooved and perforated on the left side almost certainly for the passage of segmental blood vessels. A similar pathway on dorsal vertebrae of *Eryops* could easily have been continued along the tops of the transverse processes (p. 20), behind the well-defined ridge already described, then dropping behind the rib blades almost exactly as Panchen describes and illustrates (1967: fig. 5A). Since the courses of segmental blood vessels have rarely been preserved in labyrinthodont vertebrae (Panchen, 1967: 28), these three clearly marked caudal vertebrae assume a special significance to our understanding of vertebrae and muscle segments in *Eryops*.

The broadly flat form and orientation of most of the trunk ribs in *Eryops* probably did not allow for much lateral undulation, such as suggested by Thomson and Bossy (1970: 11) for *Ichthyostega*. The tail, however, would have served as an excellent swimming organ; reconstructions that show it as flexible and leaning toward one side on land may be close to the truth. That it was strengthened by dorsal tendons seems likely from the bifurcate nature of some of the spines.

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